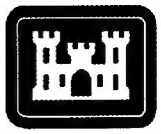
ERDC/EL TR-01-5



US Army Corps
of Engineers®
Engineer Research and
Development Center

Aquatic Plant Control Research Program

A Simulation Model for Growth of the Submersed Aquatic Macrophyte American Wildcelery (*Vallisneria americana* Michx.)

Elly P. H. Best and William A. Boyd

March 2001

Environmental Laboratory

The contents of this report are not to be used for advertising, publication, or promotional purposes. Citation of trade names does not constitute an official endorsement or approval of the use of such commercial products.

The findings of this report are not to be construed as an official Department of the Army position, unless so designated by other authorized documents.

PRINTED ON RECYCLED PAPER

Aquatic Plant Control Research Program

ERDC/EL TR-01-5
March 2001

A Simulation Model for Growth of the Submersed Aquatic Macrophyte American Wildcelery (*Vallisneria americana* Michx.)

by Elly P. H. Best and William A. Boyd

Environmental Laboratory
U.S. Army Engineer Research and Development Center
3909 Halls Ferry Road
Vicksburg, MS 39180-6199

Final report

Prepared for U.S. Army Corps of Engineers
Washington, DC 20314-1000

Contents

List of Figures

List of Tables

Preface

The work reported herein was conducted as part of the Aquatic Plant Control Research Program (APCRP) and the Upper Mississippi River – Illinois Waterway (UMR-IWW) System Navigation Study. The APCRP is sponsored by Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Research and Development Center (ERDC) under the purview of the Environmental Laboratory (EL), Vicksburg, MS. The UMR-IWW System Navigation Study is being conducted by the U.S. Army Engineer Districts, Rock Island, St. Louis, and St. Paul, under the authority of Section 216 of the Flood Control Act of 1970. Funding for the APCRP was provided under Department of Army Appropriation Number 96X3122, Construction General. The APCRP is managed under the Center for Aquatic Plant Research and Technology (CAPRT), Dr. John W. Barko, Director. Mr. Robert C. Gunkel, Jr., was Assistant Director, CAPRT. Technical Monitor during this study was Mr. Timothy R. Toplisek, HQUSACE.

The work described herein was performed at ERDC, EL, Environmental Processes and Effects Division (EPED), by Dr. Elly P. H. Best, Fates and Effects Branch (ES-F), with programming assistance from Mr. William A. Boyd, Ecosystems Processes and Effects Branch (EPEB). Ms. Anne B. Stewart, AScI Corporation, assisted with the graphics. Dr. Best and Mr. Boyd prepared this report. Dr. Carl Korschgen (Upper Midwest Environmental Sciences Center, U.S. Geological Survey, La Crosse, WI) provided an external technical review. The report was reviewed internally by Drs. John D. Madsen and Robert Kennedy, EPEB.

This investigation was performed under the direct supervision of Dr. Bobby L. Folsom, Jr., Chief, Fate and Effects Branch, and the general supervision of Dr. Richard E. Price, Chief, EPED, and Dr. John W. Keeley, Acting Director, EL.

At the time of publication of this report, Director of ERDC was Dr. James R. Houston. Commander was COL James S. Weller, EN.

This report should be cited as follows:

Best, E. P. H., and Boyd, W. A. (2001). "A simulation model for growth of the submersed aquatic macrophyte American wildcelery (*Vallisneria americana* Michx.)," ERDC/EL TR-01-5, U.S. Army Engineer Research and Development Center, Vicksburg, MS.

1 Introduction

General

The degree to which aquatic macrophytes influence the ecosystem is proportional to plant mass and depends on plant species and physicochemical factors. Therefore, predictions of the environmental impact of management measures on aquatic plant communities should be based on accurate estimates of (a) plant species and mass, and its pertinent physiological properties, (b) the contribution of the plant to the various food chains, and (c) the contribution of the decay of the plant to biogeochemical cycling and oxygen regime. A simulation model for metabolism and growth of aquatic macrophyte community types may serve as a useful tool in this respect.

Although the number of simulation models for growth of monotypic, submersed macrophyte communities is increasing (e.g. Titus et al. 1975; Best 1981; Collins and Wlosinski 1985; Best and Jacobs 1990; Hootsmans 1991; Scheffer, Bakema, and Wortelboer 1993; Best and Boyd 1996; Best and Boyd 1999a), it is still relatively low compared with that for terrestrial vegetation. The current model has been developed because none of the existing models were suitable to simulate the behavior of a monotypic American wildcelery community under various environmental and climatological conditions over a period ranging from one season to several years.

Taxonomy and Distribution of American Wildcelery within the United States

The submersed, rooted aquatic macrophyte *Vallisneria americana* Michx. or American wildcelery belongs to the monocotyledonous family Hydrocharitaceae. In 1803 Michaux first described the North American Vallisneria plant as a distinct species, *Vallisneria americana* (Fernald 1918). However, several authors named the plant a variety of the European species *V. spiralis* (e.g., Gray 1848, 1874; Chapman 1883; Britton and Brown 1913), with flower morphology and pollination mechanisms being the major differences between both species (Svedelius 1932; Kausik 1939). Sculthorpe (1967) suggested that *V. americana* may be a geographical race of *V. spiralis*. In contemporary floras (Fernald 1950; Gleason 1968), only *V. americana* is cited in eastern North America south to Florida and Texas (Gulf States). More recently (Correll and Correll 1972), it has been reported from Texas, New Mexico, and Arizona in the southwestern

United States. The large robust plants from central and south Florida, identified as *V. neotropicalis* (Marie-Victorin 1943; Long and Lakela 1971), were treated as giant variants of *V. americana* by Godfrey and Wooten (1997). The latter authors suggest that the large size of plants is a consequence of the relatively cool and almost constant temperature (approximately 21 °C) throughout the year of the often spring-fed streams and that size differences are correlated with the age of the individual plants or clones. As probable synonyms *V. spiralis*, *V. gigantea*, *V. asiatica*, *V. subulispatha*, *V. neotropicalis*, *V. higoensis*, and *V. natans* are listed (Lowden 1982; Catling et al. 1994).

Evolutionary trends indicate that the common unisexual flowers and the dioecious condition of the genus have been derived from a primitive bisexual flower. Although bisexual, male and female populations occur in North America, female populations predominate (Lowden 1982). Hereafter, American wildcelery will be referred to simply as wildcelery.

Wildcelery occurs in circumneutral fresh to slightly saline waters with an alkalinity ranging from 0 to 300 mg L^{-1}, at depths of 0.1 to 7 m, and rooted in a variety of sediment types (Titus and Stephens 1983; Korschgen and Green 1988; Godfrey and Wooten 1997; Nichols 1999). It is sometimes considered a nuisance plant in areas with a warm climate, where it may interfere with human utilization of freshwater resources. However, the latter phenomenon is merely observed in shallow areas because of the limited elongation potential of the plant resulting in inability to concentrate photoreceptive biomass at or near the water surface in low light environments (Barko, Hardin, and Matthews 1984). Wildcelery typically concentrates >60 percent of its biomass in the lower 0.3-m layers of the water column. All parts of wildcelery are important as food for waterfowl, but particularly the subterranean tubers are favored by Canvasback ducks (Lovvorn 1989; Lovvorn and Gillingham 1996).

The simulation model developed in this study concerns American wildcelery. The following appendices are included in this report: Model Listing as Appendix A, Variable Listing as Appendix B, and Manipulation of Literature Data Used for the Model Equations as Appendix C. A user manual is published separately (Best and Boyd 2001a).

2 VALLA: Description of Model

Modeling Concepts

The VALLA (Version 1.0) model simulates growth of a typical dioecious American wildcelery community. In the model, growth is considered to be the plant dry matter accumulation including subterranean tubers, under ample supply of nitrogen and phosphorus, in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. At least one plant cohort waxes and wanes per season in different climatological regions, varying from temperate to tropical. The rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. The rate of CO_2 assimilation (photosynthesis) of the plant community depends on the radiant energy absorbed by the canopy, which is a function of incoming radiation, reflection at the water surface and attenuation by the water column, attenuation by the plant material, and leaf area of the community. From the absorbed radiation, the photosynthetic characteristics of individual shoot tips and the pH-determined CO_2 availability, the daily rate of gross CO_2 assimilation of the community is calculated. These calculations are executed in a set of subroutines added to the model.

Part of the carbohydrates produced is used to maintain the existing biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the process of conversion, part of the weight is lost in respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors defined as a function of the phenological cycle of the community. The dry weights of the plant organs are obtained by integration of their growth rates over time. The plant winters through tubers in the sediment without or with biomass present. All calculations are performed on a square meter basis. Since environmental factors and plant growth characteristics vary with depth, in the model the water column and associated growth-related processes have been partitioned in 0.10-m depth classes (Titus et al. 1975).

Seed formation has not been included in the model, because its role in maintaining an existing wildcelery community at the same location is minimal (Titus and Stephens 1983; Korschgen and Green 1988; Titus and Hoover 1991; Catling et al. 1994). However, dispersal and colonization of new habitats by seeds are recognized as important characteristics of wildcelery (Lokker et al. 1994; Kimber, Korschgen, and Van der Valk 1995). The latter processes are

better described using other modeling approaches (based on logistic regression or on descriptions of population dynamics varying in time and in space), as discussed by Scheffer (1991).

VALLA requires as input physiological properties of the plant community (in this case of wildcelery) and of the actual environmental and weather conditions at the site. These properties are characterized by geographical longitude and latitude, i.e., height of the water column, water temperatures (optional), alkalinity, pH, and daily maximum and minimum temperatures and irradiance for each day of the year. It can be run for periods of 1 to 5 years.

Modeling Approach

VALLA is a mechanistic model that explains plant growth on the basis of the underlying processes, such as CO_2 assimilation, and respiration, as influenced by environmental conditions. This type of model follows the state-variable approach in that it is based on the assumption that the state of each system can be quantified at any moment and that changes in the state can be described by mathematical equations. In this type of model, state, rate, and driving variables are distinguished. State variables are quantities such as biomass and number of individuals of a population. Driving variables characterize the effect of environment on the system at its boundaries, such as climate and food supply. Each state variable is associated with rate variables that characterize its rate of change at a certain instant, as a result of specific processes. These variables represent flows of material between state variables, the values of which are calculated from the state and driving variables according to knowledge of the physical, chemical, and biological processes involved. After calculating the values of all rate variables, they are then used to calculate the state variables according to the scheme: state variable at time $t + \Delta t$ equals state variable at time t plus the rate at time t multiplied by Δt. This procedure, called numerical integration, gives the new values of the state variables, from which the calculation of rate variables is repeated. To avoid instabilities, the time interval Δt must be small enough so that the rates do not change materially within this period. This is generally the case when the time interval of integration is smaller than one-tenth of the "time coefficient" or "response time." This characteristic time of a system is equal to the inverse of the most rapid relative rate of change of one of its state variables. The smaller the time coefficient, the smaller the time interval of integration (Rabbinge and De Wit 1989).

The predictive ability of mechanistic models does not always live up to expectations. It should be realized, however, that each parameter estimate and process formulation has its own uncertainty, and that uncertainties in parameter estimates may accumulate in the prediction of the final yield. The primary aim of this model is to increase insight in the system studied by quantitatively integrating the current knowledge in a dynamic simulation model. By studying the behavior of such a model, better insight in the real system is gained.

Implementation

The VALLA model was implemented as a FORTRAN77 program. For numerical integration, the Runge-Kutta technique is used, which allows employing a variable time-step. The program, as it is being run, integrates the equations once per day in the main subroutine MODEL (see Figure 1); once per second in the subroutines calculating day length and instantaneous irradiance (ASTRO) and instantaneous gross assimilation (ASSIM), and at three times of the day in the subroutine calculating daily total gross assimilation (TOTASS; Gaussian integration). Instantaneous gross assimilation is calculated per second and converted to hourly rates within ASSIM.

Model approach and organization are similar to those used for agricultural crops (SUCROS1; Goudriaan, Van Keulen, and Van Laar 1992). Several features of a generic growth model for submersed angiosperms, SUBANG (Best and Jacobs 1990), and for other submersed plant species, HYDRIL (Best and Boyd 1996; Boyd and Best 1996); and MILFO (Best and Boyd 1999a,b) have been used.

VALLA runs within a FORTRAN SIMULATION ENVIRONMENT (FSE) shell, Version 2.1, to enable easy handling of input and output files and rapid visualization of the simulation results (Van Kraalingen 1995). It can be executed on IBM PC- ATs and compatibles as a stand-alone version. Because of its language and simple structure, it will generally be compatible with ecosystem models that accept FORTRAN.

The organization of the model and its subroutines in combination with the FSE shell is illustrated in Figure 1.

Model Features

Features of VALLA are:

a. Phenology is tied indirectly to air temperature through development rate, and is, therefore, independent of day of year; thus, the model can be used under climatological conditions ranging from temperate to tropical.

b. Plant growth starts from the subterranean tuber bank alone, which may range from tuber densities as low as 1 to a tuber bank with wintering plants present.

c. One or more plant cohorts can be active in temperate as well as tropical climates; in case of plantlet death during prolonged periods of negative net photosynthesis early in the season, the dead plant cohort is succeeded by the next sprouting plant cohort.

d. Photosynthetic response is to instantaneous irradiance.

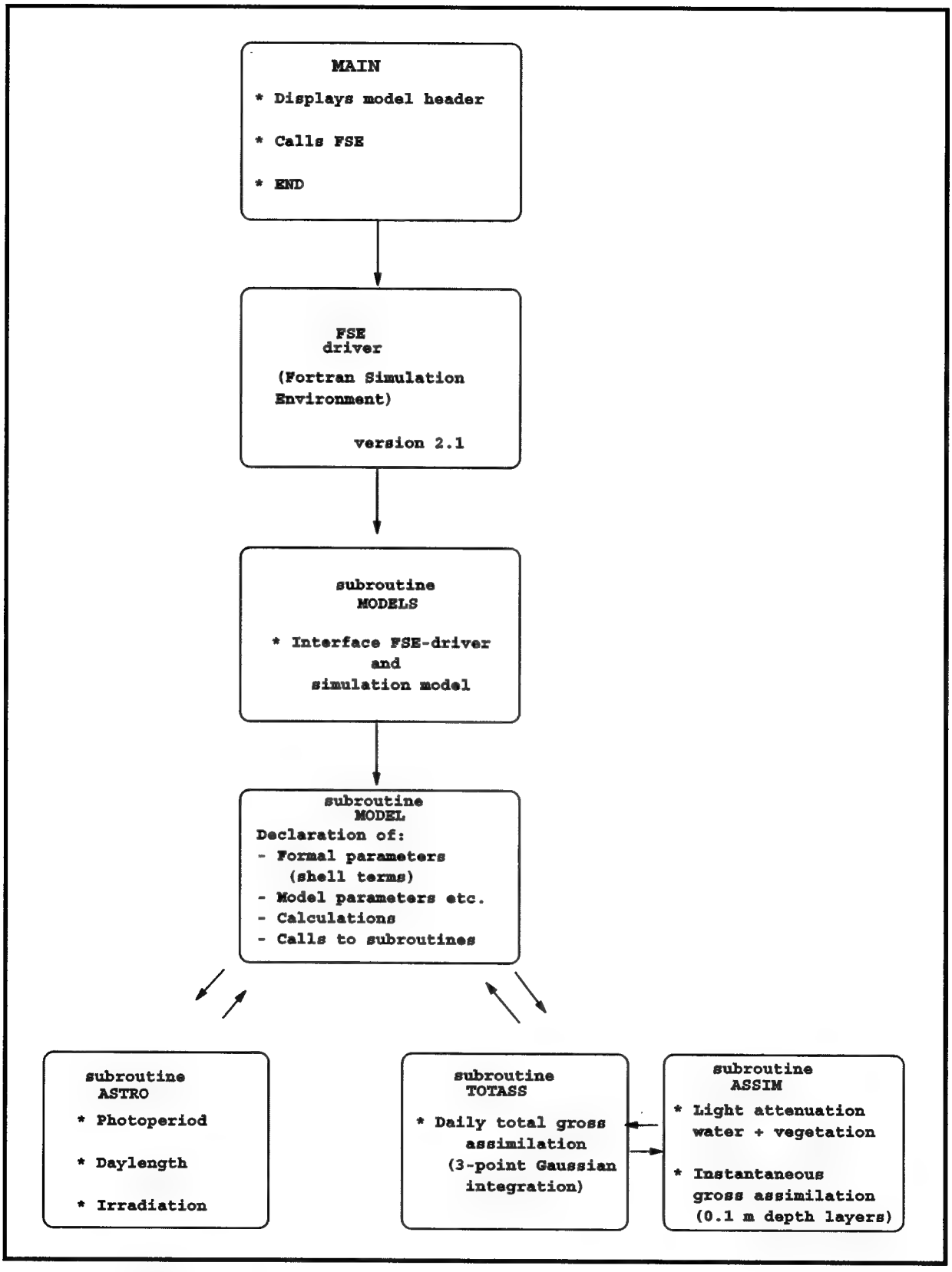


Figure 1. Relational diagram illustrating the organization of the model VALLA and its subroutines in combination with the FSE shell

e. Air or water temperatures must be used to run the model. When air temperatures are used, the lag period between air and (calculated) water temperatures can be varied between 1 and 7 days; this is an important feature for application in water bodies varying in depth, with large groundwater inputs, etc.

f. The model can be used for communities at water depths, that may vary between years and daily within the year, with depths ranging from 0.2 to 6.0 m; this is an important feature for application in reservoirs and rivers.

g. Plant parameter values and climatological variables can be easily changed.

h. Effects of removal of plant biomass, through cutting, and of tubers, through grazing, can be calculated if desired.

3 Model Processes

Morphology, Phenological Cycle, and Development

Morphology and phenological cycle of wildcelery

The dioecious wildcelery biotype is anchored to the sediment by fibrous roots. In summer, the plant has a short stem axis, bearing a variable number of stolons. The plant forms a rosette on top of the sediment with up to 1.2-m-long, linear strap- to tape-shaped leaves, submersed or floating at the water surface (Lowden 1982; Titus and Stephens 1983; Korschgen and Green 1988). The dioecious biotype can propagate sexually by seeds, but a most important means of propagation appears to be vegetatively by tubers in North America. Tubers are relatively small, dormant organs that develop on most stolons under special day length and temperature conditions in autumn and that grow down into the sediment. Tubers are composed of a small amount of dividing tissue surrounded by several fleshy leaves. The parent plants senesce and disintegrate at the end of the growth season, and only the tubers hibernate within the sediment until their emergence the following spring, which completes the annual growth cycle. Tubers are exhausted and disintegrate during the summer in which they were formed. Flowering of wildcelery occurs once a year, from late June to August in the northern hemisphere (Donnermeyer 1982; Titus and Stephens 1983; Donnermeyer and Smart 1985). Flowering usually coincides with peak biomass and is followed immediately by sloughing. The production of viable seeds requires pollination on the water surface with free-floating male flowers tipping into the surface depression created by the larger, attached female flowers. Fruits mature under water (Lowden 1982). Seeds can be important in long distance dispersal and as insurance against local extinction. Seed germination appears to be insensitive to light level and occurs optimally directly from the pods (Personal Communication, April 2000, M. Smart, U.S. Army Research and Development Center (ERDC), Lewisville, TX). In contrast, seedling establishment requires a light level of at least 9 percent of surface irradiance in mimicked environmental conditions (Kimber, Korschgen, and Van der Valk 1995), and seedling establishment in the field is suggested to be rare in the northern United States (Titus and Stephens 1983). The rarity of seedling establishment in the northern United States is a result of the relatively high optimum temperature for germination, 30 to 35 °C; (Choudhuri 1966), but it has frequently been observed in Texas reservoirs (McFarland and Rogers 1998; Personal Communication, April 2000, M. Smart, ERDC, Lewisville, TX).

Description of development and phenological cycle in VALLA

The phenology of a plant community, for which the development phase can be used as a measure, quantifies physiological age and is related to its morphological appearance. The development phase can not be expressed simply as chronological age, because several environmental factors such as temperature and stress (e.g., nutrients, grazing), can speed up or reduce the rate of phenological development. Contrary to what is suggested by intuition, the rate of plant growth per se has no effect on phenological development, as long as the growth rate is not very low (Penning de Vries et al. 1989b, and citations therein). The concept of development phase is used to characterize the whole plant community; it is not appropriate for individual organs.

The response of developmental rate to temperature in the current model is in accordance with the day-degree hypothesis (Thornley and Johnson 1990a). The idea is as follows. The mean temperature T_i for each day i is measured, and a sum h is formed according to the following equation:

$$h = \sum_{i=1}^{j} (\overline{T}_i - T_c) \tag{1}$$

which includes only those terms where $\overline{T}_i$ is above some threshold value T_c. When h reaches a particular value, this signifies that a phase in development is complete, and this is generally associated with a biological event that occurs over a short period of time and is readily observed. The day-degree sum h essentially integrates some underlying temperature-dependent processes. For wildcelery, for example, there are various phases in the development of the plant, and the day-degree sum has a certain value for the successful completion of each. The temperature threshold T_c may be different for each of these phases. The approach is based on the notion of a developmental rate, whose response to temperature is approximately linear over a restricted temperature range. Comparison with actual temperature responses found in agricultural crops suggests that this is not unreasonable, and the method works well in practice. It is implicitly assumed that the organ possesses a developmental clock that is proceeding at the rate k_d. In general, it is to be expected that the development rate k_d may depend on a number of quantities. This can be represented by the following equation:

$$k_d = f(V, P, E) \tag{2}$$

in which f represents some function of the state variables V, parameters P, and environmental quantities E. The day-degree-sum rule works because the most important environmental variable is temperature, and the response to temperature is approximately linear.

The phenological cycle is described using wildcelery in Chenango Lake, New York, in 1978 as an example (Titus and Stephens 1983). Plant data of this year were chosen after verifying climatological conditions did not deviate from the usual at that site.

Development phase (DVS) is a state variable in VALLA. The development phase is dimensionless, and its value increases gradually within a growing season. The development rate has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase. In the model, the temperature affecting development of wildcelery can be chosen as equal to the daily average air temperature at the height of the growing point of the shoots, with a user-defined lag-period to correct for deviations in temperature of the water body in which the aquatic community grows compared with air temperatures (7 days is nominal). It is more accurate to use water temperatures for this purpose, but since water temperatures are not always available for the site for which the user wants to run the model, VALLA can be run using either one.

Temperature can have a different effect on the rate of phenological development in the vegetative phase and in the reproductive phase. These differences indicate that the physiological process of development may not be the same before and after anthesis. Only one flowering period occurs in a temperate climate, i.e., from the end of June to August (Donnermeyer 1982; Donnermeyer and Smart 1985; Titus and Stephens 1983). Flowering behavior in a tropical climate is presumed to be similar to that in a temperate climate, but supporting data are lacking (Haller 1974).

The following development rates were derived from the Chenango Lake field data (Titus and Stephens 1983): 0.015 d^{-1} prior to the flowering period of 0.040 d^{-1} subsequently, at a reference temperature of 30 °C and a temperature threshold of 3 °C. These development rates are considered as typical for temperate regions. They are in the same order of magnitude as those found for the other submersed hydrilla, Eurasian water-milfoil, and sago pondweed (Best and Boyd 1996; Best and Boyd 1999a; Best and Boyd 2001a), but higher than that found for the terrestrial, tuber-forming, sweet potato (development rate of 0.006 d^{-1} at a reference temperature of 27 °C; (Kooman 1995)). For wildcelery populations in the tropics, the same development rates and timings as in temperate regions were applicable (Haller 1974).

The development phase has the value 0.0 when the simulation starts at the first Julian day number (Table 1). The simulation starts using an observed tuber density, with a certain, chosen (this chapter, section on Wintering and Sprouting of Tuber Bank) individual tuber weight as initial values. The quantities of leaves, stems, and roots are set equal to 0. If simulation of a wildcelery community at another site is desired, the simulation can start also with wintering plants present; first, however, initial quantities of plant organs must be calculated.

For a wildcelery community in a temperate climate, the sprouting of the tubers, i.e. the initiation of growth activity, occurs at DVS 0.292. Sprouts of the first plant cohort develop through remobilization of carbohydrates from the tubers. The sprouts elongate rapidly up to the preset maximum plant height of 1.2 m or to the water surface in cases where water depth is < 1.2 m, and subsequently follow a typical, inverted umbrella-shaped, spatial distribution within the water column. Anthesis is initiated at DVS 1.000 and finishes at DVS 2.000 just before new tubers are initiated. Tubers can be formed directly when initiated, in contrast to hydrilla where tuber formation lags behind tuber initiation (Best and Boyd 1996). Tuber formation, downward translocation and senescence set in at

Table 1
Relationship between DVS of Wildcelery, Day of Year and 3 °C Day-Degree Sum in a Temperate Climate (DVRVT= 0.015; DVRRT= 0.040)

Developmental Phase			
Description	DVS Value	Day Number	3 °C Day-Degree Sum
First Julian day number → tuber sprouting and initiation elongation	0 -> 0.291	0 -> 105	1 -> 270
Tuber sprouting and initial elongation → Leaf expansion	0.292 -> 0.875	106 -> 180	271 ->1,215
Leaf expansion → floral initiation and anthesis	0.876 - >1.000	181 - >191	1,216 -> 1,415
Floral initiation and anthesis -> induction of tuber formation, tuber formation and senescence	1.001 -> 2.000	192 -> 227	1,416-> 2,072
Tuber formation and senescence → senesced	2.001 -> 4.008	228 -> 365	2,073 -> 3,167
Senesced	4.008	365	3,167

Note: Calibration was on field data on biomass and water transparency from Chenango Lake, New York, 1978 (Titus and Stephens 1983), and climatological data from Binghamton (air temperatures) and Ithaca (irradiance), New York, 1978.

DVS 2.001 and continue until the end of the year. The development phase is dimensionless, and its value increases gradually. The development rate has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase (Table 1).

Wildcelery plants in tropical regions behave similar in terms of DVS to those in temperate regions, except that tropical plants require on average a 1.6 × higher 3-°C-day-degree sum to complete their individual life cycle than temperate cohorts.

Maximum Biomass and Plant Density

Seasonal biomass maxima can vary considerably over time and space. In temperate climates usually one biomass peak per growth season was found, which occurred just before flowering. For subtropical to tropical areas in Florida a relatively constant, high biomass has been suggested (Godfrey and Wooten 1997). The highest standing crop of 496 g DW m^{-2} has been found in 1.5-m-deep experimental ponds, in Orange County, Florida (tropical, i.e. longitude 81° 20' W, latitude 28° 30' N; (Haller 1974)), while somewhat lower values have been reported for the more northern University Bay, Wisconsin, in 1976 (344 g DW m^{-2} at a 1.2- to 1.5-m anchorage depth; longitude 89° 20' W, latitude 43° 08' N; (Titus and Adams 1979b)) and Lake Biwa, Japan, in 1969 (253 g DW m^{-2} at a 0.73-m anchorage depth; approximate longitude 136° E, latitude 35° 30' N; (Ikusima 1970)). The maximum biomass value published has been used to form the upper limit of plant biomass in the model.

Wildcelery exhibits clonal growth consisting of the production through the season of potentially interdependent, nonperennating rosettes, followed by the development of tubers, which become independent ramets upon disintegration of

the parent plants in early fall. Since currently no evidence of interdependency of wildcelery rosettes has been published, all intact rosettes and tubers produced in one season from an initial tuber are viewed as individual plants in the model. Typical plant density is 30 plants m^{-2}. It has been computed by dividing the maximum standing crop of an established, monotypic wildcelery vegetation (50.1 g DW m^{-2}) by the average weight of an individual rosette with neighbor plants (1.65 g DW m^{-2}) in Chenango Lake, New York (Titus and Stephens 1983). Other literature reviewed did not provide sufficiently detailed information to enable calculations of plant density. Typical plant density indicates in this case, that it is possible that at some point in time different plant densities may occur, but that a typical established, monotypic wildcelery vegetation optimizes at 30 plants m^{-2}. Lower densities may occur in the establishment phase, where some plants may not yet have neighbors and become relatively large, while higher plant densities may occur early in the season when >30 tubers m^{-2} have sprouted but the plantlets are subsequently thinned to 30 plants m^{-2} by self-shading of the vegetation.

In VALLA, plant density has been set to 30 plants m^{-2}. This implies that plant density at the beginning of the growth season is in principle 30 plants m^{-2}. Thus, the number of sprouting tubers in the tuber bank is 30 plants m^{-2}, while the remaining tubers continue to senesce. However, at tuber bank densities lower than 30 tubers m^{-2}, the number of sprouting tubers is recalculated and set equal to the actual tuber bank density. If wintering plants are present, plant biomass is redistributed over 30 plants m^{-2}.

Wintering and Sprouting of Tuber Bank

Tubers are the main storage organs for carbohydrates in wintering wildcelery in a temperate climate. Basal stem sections can play a similar role as tubers in a tropical climate (Haller 1974). In tubers, concentrations of starch may reach 20 percent and concentrations of total nonstructural carbohydrates (TNC) may reach 42 percent dry weight (Titus and Adams 1979b). Tuber biomass is 0 in early summer and reaches a maximum in autumn. It is difficult to present an accurate estimate of the tuber biomass range because in most papers either plant biomass and tuber numbers without tuber biomass, or tuber numbers and biomass without plants are presented. Another complicating factor is that individual tuber weight varies substantially.

Tuber densities in the wildcelery tuber banks vary over a large range, from 0 in early summer to a maximum of 450 m^{-2} in autumn. This is probably largely because of (a) the patchy spatial distribution of the community over the water body, (b) limited number of replicate samples taken (Spencer, Ksander, and Whitehand 1994), and (c) between site variation of anchorage depth of the vegetation.

The following densities have been published: (a) 101 tubers m^{-2} in Lake Mendota, Wisconsin (Titus and Adams 1979b), 170 tubers m^{-2} in Pool 9 of the Upper Mississippi River, Wisconsin (Donnermeyer 1982); (b) 233 tubers m^{-2} in the Lower Detroit River, Michigan (Korschgen and Green 1988); (c) 330 to 450 tubers m^{-2} calculated by multiplication of typical plant density and measured

range of concomitantly initiated tuber number of 11 to 15 plant $^{-1}$ (Titus and Stephens 1983); and (d) 115 to 1140 tubers m^{-2} in the shallow (<1-m-deep) Lake Mattamuskeet, North Carolina (Lovvorn and Gillingham 1996).

Published tuber weights (g dry weight tuber^{-1}) are: (a) 0.04 to 0.18 g, various North American water bodies (Korschgen and Green 1988; Korschgen, Green, and Kenow 1997); (b) an average of 0.055 g (Chenango Lake, New York, 1.4-m anchorage depth (Titus and Stephens 1983)); (c) an average of 0.07 g (Lake George, New York, 2- to 4-m anchorage depth, (Personal Communication, April 2000, ERDC, J. D. Madsen, Vicksburg, MS)); and (d) maximally 0.18 g just after tuber completion (Pool 9 Upper Mississippi River, Wisconsin, 1.1-m anchorage depth (Donnermeyer 1982; Takekawa 1987)). Individual tuber weight and number of tubers concurrently formed by each plant depend on the light level at which the plant grows. Individual tuber weight decreased almost linearly with increasing suspended solids concentration of the water column and, thus, decreasing light level (from 0.102 to <0.01 g dry weight tuber^{-1}), and parabolically with tuber number concurrently formed per plant, from 6.5 to 0.5 g (Korschgen, Green, and Kenow 1997), Figure 2.

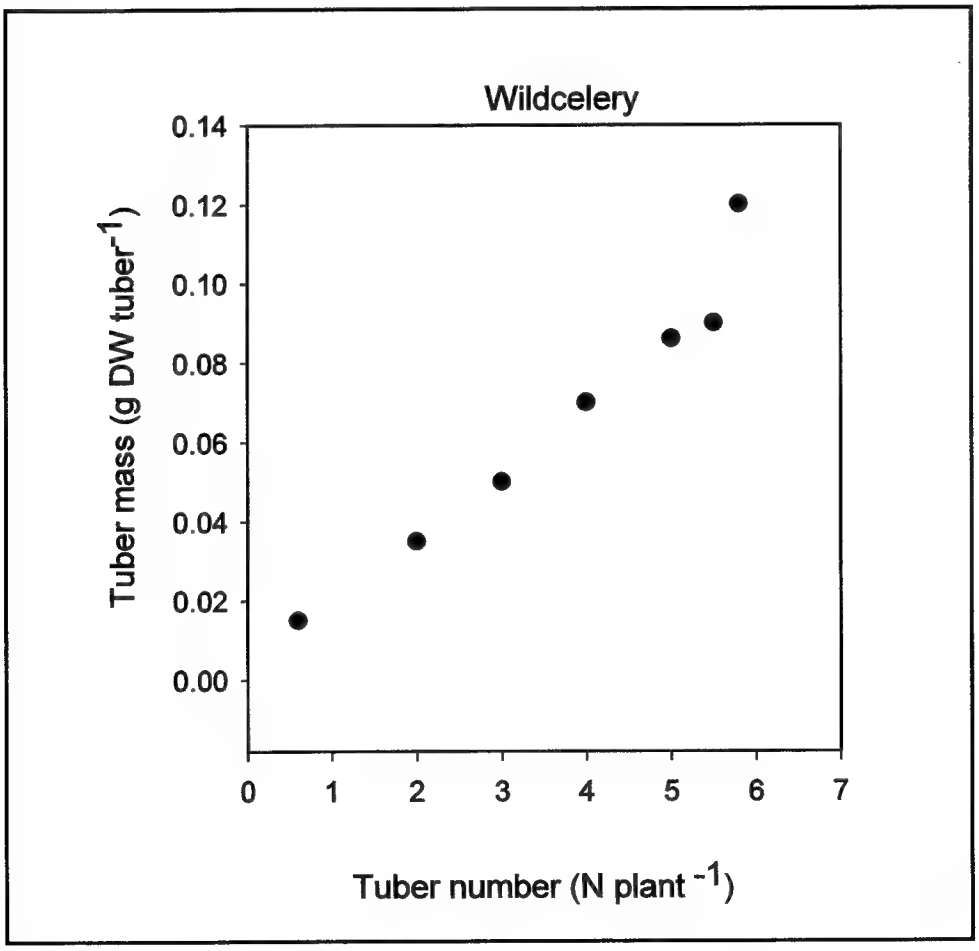


Figure 2. The relationship between tuber number concurrently initiated per plant and tuber size for wildcelery (modified from Donnermeyer and Smart 1985; Korschgen, Green, and Kenow 1997)

Tubers lie dormant if not disturbed, and it is, therefore, to be expected that maintenance processes proceed at a very low level of activity. Tuber weight may decrease by tuber death and by the sprouting of tubers, which transform into plants. Tuber density may decrease by grazing by waterfowl and other animals. Both tuber weight and density may increase by the formation of new tubers (this chapter, section on Induction and Formation of New Tubers).

Sprouting potential of the tubers is usually high in a temperate climate, being $\leq$80 percent. Sprouting frequency in an established community is probably not important, unless it is very low, as long as the typical plant density of 30 plants m^{-2} is somehow reached, since plant density tends to play a lesser role in biomass production compared to space availability. Actual sprouting frequency under natural conditions is unknown. Sprouting was not affected by day length, but it was higher under illumination than in darkness. It was prevented by temperatures $\leq$ 5 °C, optimal between 15 and 25 °C, and maximal at 20 and 25 °C (Personal Communication, April 2000, ERDC, J. D. Madsen, Vicksburg, MS). Sprouting takes place early in the season. The earliest date mentioned is the period between mid-April and the end of May, when the first young rosettes developed in Pool 9 of the Upper Mississippi River, Wisconsin, in 1980-81(Donnermeyer 1982).

Death rates of tubers have not been published. The value for the relative death rate of tubers, *RDTU*, was found by applying the same differential equation as commonly used for simple exponential growth, to describe continuous exponential decrease in tuber number, with a negative specific decrease rate (Thornley and Johnson 1990b; Hunt 1982). An *RDTU* of 0.018 d^{-1} (on number basis) was found for the wildcelery population in Chenango Lake, New York (Titus and Stephens 1983). The latter *RDTU* value is far lower than that of 0.36 d^{-1} for hydrilla tubers, that was estimated from simulations alone because virtually no seasonal changes in hydrilla tuber data had been published at that time (Best and Boyd 1996). Both plant species are expected to lose tubers through grazing by waterfowl. However, the relatively lower loss in wildcelery may be explained by the relatively low tuber bank density of this plant (5 to 10 times lower than in hydrilla) which may discourage foraging by waterfowl because it may require a relatively long search time (Lovvorn1989; Lovvorn and Gillingham 1996).

Higher temperatures expedite turnover rates of plant tissues and increase maintenance costs. A temperature increase of 10 °C usually increases maintenance respiration by a factor of about 2 (up to temperatures that usually kill plants (45 to 60 °C; $Q_{10} = 2$ at a reference temperature of 20 °C (Penning de Vries et al. 1989a)). The value of 2 for a Q_{10} appears to be a reasonable average, but lower and higher values have also been reported (Amthor 1984).

In VALLA, initial tuber biomass has been set at 20.97 g dry weight m^{-2}. The latter value was calculated by multiplication of measured tuber number m^{-2} at 1.4-m rooting depth in Chenango Lake (233 m^{-2}; Titus and Stephens 1983) and selected, optimal (Figure 2) tuber weight (0.09-g dry weight $tuber^{-1}$).

Sprouting is a function of development phase through the 3-°C day-degree sum; it occurs between *DVS* 0.292 and the flowering period of the plant population. Sprouting frequency has been set equal to the number of plants per surface area, i.e., at 30 sprouts m^{-2}.

The relative tuber death rate is set at 0.018 d^{-1}. It is presumed to be influenced by temperature through a relative, effective temperature function, *TEFF*. This function describes processes relative to a reference temperature of 20 °C at which the function has the value of 1, to increase with a Q_{10} of 2 at temperatures>20 °C, to increase between 0 and 5 °C from 0.0001 to 0.5, and to decrease with a Q_{10} of 2 at temperatures<20 °C. A similar approach to account for temperature effects on maintenance respiration has been followed by Thornley and Johnson (1990a).

Initial Growth of Sprouts

Tubers sprout and plantlets initially elongate, depleting the tuber carbohydrate reserves (up to 42 percent DW) (Titus and Adams 1979b). Sprouting can only occur in tubers weighing at least 0.003 g DW $tuber^{-1}$ (Donnermeyer and Smart 1985; Personal Communication, April 2000, J. D. Madsen, ERDC, Vicksburg, MS).

Whether or not these plantlets survive at the plant height they can maximally reach by merely exhausting their carbohydrate reserves depends on the size and the carbohydrate efflux due to growth respiration of the tuber and the carbohydrate influx in the plants because of photosynthesis.

The elongation potential of sprouts emerging from tubers is limited, i.e., 0.44 m (range 0.04 to 0.18 g DW $tuber^{-1}$) (Korschgen and Green 1988; Korschgen, Green, and Kenow 1997). Thus, plants can rise to a 0.1-m-depth layer in the water column only when they can fill that layer with a minimum of 0.0091- or maximum of 0.041-g plant DW.

Respiration of tubers is low when in a dormant state. A rate of 0.00391 g CO_2 $tuber^{-1}$ day^{-1} at 10 °C was estimated for a 0.09-g DW dormant tuber. This is based on the facts that: (a) respiratory behavior in wildcelery tubers is presumed to be similar to that of sago pondweed tubers of similar size and chemical composition; (b) dormant tuber respiration rate is 0.003623 g CO_2 g DW^{-1} h^{-1} at 20 °C (E. P. H. Best, unpublished); and (c) temperature influences respiration as described in this chapter (see Wintering and Sprouting of Tuber Bank). This means that the latter tuber can survive for 23 days after sprouting if light for photosynthesis were lacking (0.00391 g CO_2 $tuber^{-1}$ day^{-1} × 23 days = 0.09 g tuber). Consequently, sprouting tubers of this size die after a survival period of 23 days without net photosynthesis taking place. Larger tubers have longer and smaller tubers have shorter survival periods.

In the model, tuber bank weight is calculated from initial tuber number and individual tuber weight is read from the input file.

Tubers sprout, provided conditions allowing sprouting are met, these being: (a) proper day-degree sum, and (b) sufficient tuber bank weight.

By sprouting, remobilization of tuber carbohydrates occurs, i.e., conversion of part of their carbohydrate reserves into sprout material via a relative

tuber-to-plant conversion rate (*ROC*) of the same value as used for hydrilla tubers (0.0576 g CH_2O g tuber DW^{-1} d^{-1}) (Best and Boyd 1996). These carbohydrates are allocated to the plant organs following a fixed biomass partitioning pattern (this chapter, section on Light, Photosynthesis, Maintenance, Growth and Assimilate Partitioning in Wildcelery Plants). Elongation occurs by filling each successive water layer from hydrosoil to a 1.2-m water column with the minimum shoot biomass required (0.0091 g plant dry weight $plant^{-1}$, termed *CRIFAC*). Remobilization and subsequent growth continues until the carbohydrates of the sprouting tubers are depleted.

Sprouting tubers die if the resulting plant biomass has a negative net assimilation rate over a user-defined number of days (*SURPER*; 23 days is nominal), and the program stops with a warning 'KCOUNT'.

After the death of one tuber class, one or more other tuber classes can sprout, provided tubers are available and the day-degree sum (Table 1) is lower than required for flowering. The program can resume running for the same year after pressing 'ENTER' provided the proper conditions are met.

A relational diagram illustrating the wintering and sprouting tubers of wildcelery is shown in Figure 3.

$$TWGTUB = NPL \times INTUB$$

$$NDTUB = NDTUB - (NTUBD - NTUBPD)$$

$$NTUBD = RDTU \times NDTUB \times TEFF$$

$$IF\ (DVS.\ GE.\ 0.291.\ AND.\ DVS\ .LT.\ 1.)\ THEN$$

$$IF\ (TWGTUB\ .LE.\ (0.01 \times NPL \times INTUB))\ NGTUB = 0.0$$

$$NGTUB = NPL$$

$$TWGTUB = INTGRL\ (TWGTUB, -REMOB, DELT)$$

$$REMOB = TWGTUB \times ROC \times TEFF$$

where

DVS = development phase of the plant (-)

INTUB = initial dry weight of a tuber (g DW $tuber^{-1}$)

NDTUB = dormant tuber number (dormant tubers m^{-2})

NGTUB = sprouting tuber number (sprouting tubers m^{-2})

NPL = plant density (plants m^{-2})

NTUBD = dead tuber number (dead tubers m^{-2})

NTUBPD = dead tuber number of the previous day (dead tubers m^{-2})

RDTU = relative death rate of tubers (on number basis; d^{-1})

REMOB = remobilization rate of carbohydrates (g DW m^{-2} d^{-1})

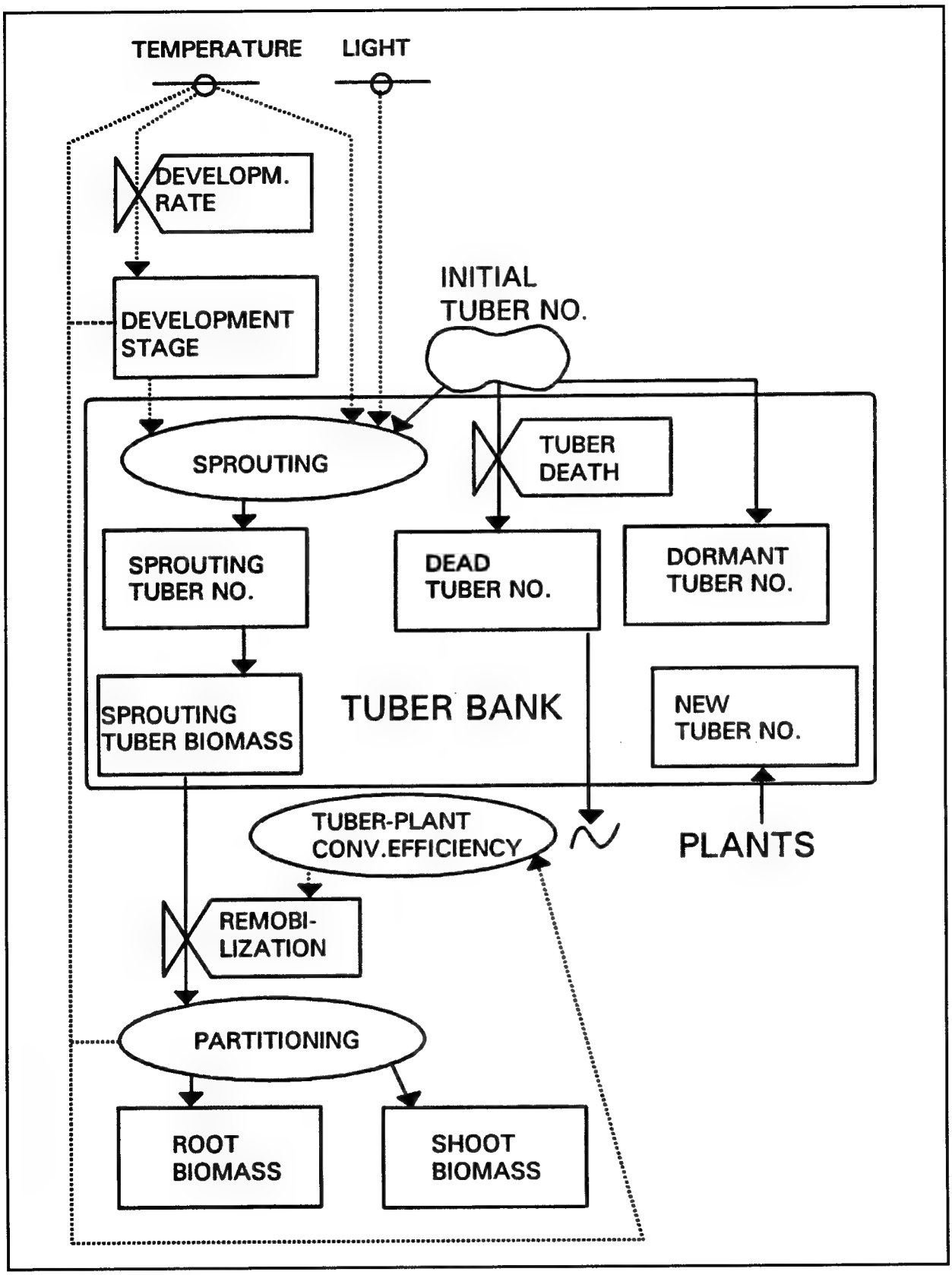


Figure 3. Relational diagram illustrating the wintering and sprouting of tubers in wildcelery

ROC = relative conversion rate of tuber into plant material (g CH_2O g DW^{-1} d^{-1})

TEFF = factor to account for temperature effect on maintenance respiration, remobilization, and maximum relative tuber growth rate (-)

TWGTUB = total dry weight of sprouting tubers (g DW m^{-2})

Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning in Wildcelery Plants

Light

Light availability is an important factor controlling the distribution and abundance of submersed macrophytes. In aquatic systems light can be attenuated rapidly by water and its suspended solids, and by macrophytes themselves. A relatively small part of the irradiance can be reflected by the water surface.

In the model, the measured daily total irradiance (wavelength 300 to 3,000 nm) is used as input. Only half of the irradiance reaching the water surface is considered to be photosynthetically active and is, therefore, used to calculate CO_2 assimilation. Six percent of the irradiance is reflected by the water surface (Golterman 1975).

The subsurface irradiance is attenuated by dissolved substances and particles within the water column resulting in a site- and season-specific extinction coefficient. Moreover, the vertical profiles of the radiation within the plant community layers are characterized. The absorbed irradiance for each horizontal community layer is derived from these profiles. The community-specific extinction coefficient, *K*, is assumed to be constant throughout the year and given a value of 0.0235 m^2 g DW^{-1} measured in the canopy of a wildcelery community in Lake Mendota, Wisconsin (Titus and Adams 1979a). Other lower, community-specific extinction coefficients of 0.0051, 0.013 to 0.019, and 0.018 m^2 g DW^{-1} have been published by Blanch, Ganf, and Walker (1998), Titus and Adams (1979a) ('vertical *K*'), and Ikusima (1970).

The incoming irradiance is attenuated by the shoots, part of which is absorbed by the photosynthetic plant organs, i.e., the leaves.

$$IRZ_{i+1} = IRZ_i \times e^{(-TL \times L - K \times SC_i)}$$

$$IABS_i = \frac{(IRZ_i - IRZ_{i+1}) \times SC_i \times K}{(K \times SC_i + TL \times L)} \qquad (3)$$

$$IABSL_i = IABS_i \times FL$$

where

FL = leaf dry matter allocation to each layer of the vegetation (relative; -)

$IABS_i$ = total irradiance absorbed in depth layer i (J m^{-2} s^{-1})

$IABSL_i$ = total irradiance absorbed by plant shoots in depth layer i (J m^{-2} s^{-1})

IRZ_i = photosynthetic active part of total irradiance on top of depth layer i (J m^{-2} s^{-1})

K = plant-specific extinction coefficient (m^2 g DW^{-1})

L = light extinction coefficient of water (m^{-1})

SC_i = shoot dry matter in depth layer i (g DW m^{-2})

TL = thickness depth layer (0.10 m)

Photosynthesis

In the model, the instantaneous rates of gross assimilation are calculated from the absorbed light energy and the photosynthesis light response of individual shoots, here used synonymously to leaves.

The photosynthesis light response of leaves is described by the exponential function

$$FGL = SC_i \times AMAX \times \left(1 - \exp\left[\frac{-EE \times IABS_i \times 3{,}600}{AMAX \times SC_i}\right]\right) \qquad (4)$$

where

$AMAX$ = actual CO_2 assimilation rate at light saturation for individual shoots (g CO_2 g DW^{-1} h^{-1})

EE = initial light-use efficiency for shoots (g CO_2 J^{-1} absorbed)

FGL = instantaneous gross assimilation rate per depth layer (g CO_2 m^{-1} h^{-1})

SC_i = shoot dry matter in depth layer i (g DW m^{-2})

For photosynthetic activity at light saturation (AMX) the value used (0.0165 g CO_2 g DW^{-1} h^{-1}) was measured by Titus (1977) in the laboratory. This value is equal to the laboratory and field AMX of Eurasian watermilfoil measured in Lake Wingra in May 1971, at pH 8 and a total alkalinity of 190 mg L^{-1}, and slightly higher than field values measured for hydrilla in water in equilibrium with atmospheric CO_2 (0.0158 g CO_2 g DW^{-1} h^{-1}) (Bowes, Holaday and Haller 1979; Van, Haller, and Bowes 1976). Light- and carbon-saturated photosynthetic rates of wildcelery can be far higher (Titus and Stone 1982; Titus, Feldman, and Grise 1990), suggesting that photosynthetic activity in lakes like Chenango and

Mendota, where dissolved inorganic carbon concentrations are in the range of 0.8 to 3.5 mmol with a pH of 7.6 to 9.4 can be carbon limited.

Gross assimilation rate at light saturation shows a distinct seasonal pattern and tends to decrease with aging (Titus 1977). Although a function describing this relationship (*AMDVST*) has been included in the model, it is not active in the nominal version (it has the value of 1), since it turned out not to be quantitatively important.

Daily changes in pH and oxygen concentrations may affect *AMX*. A reduction factor, *REDAM*, can be used to take these effects into account by reducing the *AMX* by a factor between 0 and 1 for the entire day. *REDAM* currently has the value of 1, because pH in the wildcelery communities in Chenango Lake oscillated around 8.5 (Titus and Stephens 1983), where actual and potential photosynthetic activity at light saturation are similar (Titus and Stone 1982). Sensitivity of wildcelery to changes in oxygen concentration is unknown to us and is not accounted for in the model.

Changes in temperature affect *AMX*. A fitted, relative function, *AMTMPT*, describes the effect of daytime temperature on *AMX*, which is based on the measured photosynthetic response of wildcelery to temperature and has its optimum at 32.5° C (Titus and Adams 1979a; Appendix C). A similar relationship between temperature and chlorophyll concentration was found by Barko and Filbin (1982).

For photosynthetic light-use efficiency (*EE*), a value of 11×10^{-6} g CO_2 J^{-1}, typical for C_3 plants, was used (Penning de Vries and Van Laar 1982a). Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer.

The instantaneous rate of gross assimilation over the height of the plant community is calculated by relating the assimilation rate per layer to the community-specific biomass distribution and by subsequent integration of all community layers.

The daily gross assimilation rate is calculated by using the Gaussian integration method. This method specifies the discrete points at which the value of the function to be integrated has to be calculated and the weighting factors that must be applied to these values to attain minimum deviation from the analytical solution. A three-point method performs very well for calculating daily total assimilation (Goudriaan 1986; Spitters 1986).

Maintenance, growth, and assimilate partitioning

Maintenance. Some of the carbohydrates formed are respired to provide energy for maintaining the existing plant components. The maintenance costs increase with metabolic activity, probably because of higher enzyme turnover and higher transport costs (Penning de Vries 1975).

The maintenance cost can be estimated from the chemical composition of the plant. Typical maintenance coefficients for various plant organs have been derived, based on numerous chemical determinations in agricultural crops. They typically range from 0.010 to 0.016 g CH_2O g $AFDW^{-1}$ d^{-1} (Penning de Vries and Van Laar 1982b).

In VALLA, the maintenance coefficients mentioned above are used to calculate the maintenance requirement of the plants. Maintenance respiration has been related to temperature by the same relative effective temperature function as used for the remobilization and relative tuber growth and death rates. Maintenance costs for the tubers have been discussed earlier in this chapter, section on Wintering and Sprouting of Tuber Bank.

Equations describing maintenance costs for wildcelery plants are:

$$MAINTS = 0.016 \times TWLG + 0.010 \times TWSG + 0.015 \times TWRG$$

$$MAINT = MAINTS \times TEFF \quad (5)$$

where

MAINT = maintenance respiration of the vegetation (g CH_2O m^{-2} d^{-1})

MAINTS = maintenance respiration rate of the vegetation at reference temperature (g CH_2O m^{-2} d^{-1})

TEFF = factor accounting for effect of temperature on maintenance respiration (-)

TWLG = total dry weight of live leaves (g DW m^{-2})

TWSG = total dry weight of live stems (g DW m^{-2})

TWRG = total dry weight of live roots (g DW m^{-2})

Growth. Assimilates in excess of maintenance costs are available for conversion into structural plant material. In this conversion process of the glucose molecule, CO_2 and H_2O are released. The assimilates required to produce one unit weight of any particular plant organ can be calculated from its chemical composition and the assimilate requirements of the various chemical components. Typical values are: 1.46 g CH_2O g DW^{-1} for leaves, 1.51 for stems, and 1.44 for roots (Penning de Vries and Van Laar 1982b; Penning de Vries et al.1989a), confirmed by Griffin (1994). At higher temperatures the conversion processes are accelerated, but the pathways are identical. The recently determined construction costs for several submersed plant species using a different method (Williams et al. 1987) are generally lower, ranging from 0.99 to 1.11 (Spencer, Ryan, and Ksander 1997). However, some of the latter plants are relatively poor in nitrogen and transport costs have not been included, both factors may have contributed to the lower cost found.

In VALLA the construction costs typical for agricultural plants have been used, since construction costs calculated for wildcelery leaves with an average chemical composition were similar to those in agricultural plants, i.e., 1.465 CH_2O g DW^{-1} (for calculation costs for leaves, see Appendix C), and stems and roots were presumed to be similar also.

The following equation describes growth:

$$GTW = \frac{((REMOB \times CVT) + GPHOT - TRANS - MAINT)}{ASRQ} \qquad (6)$$

where

ASRQ = assimilate requirement for plant dry matter production (g CH_2O g DW^{-1})

CVT = conversion factor of translocated dry matter into CH_2O (-)

GPHOT = daily total gross assimilation rate of the vegetation (g CH_2O m^{-2} d^{-1})

GTW = dry matter growth rate of the vegetation (plants excluding tubers; g DW m^{-2} d^{-1})

MAINT = maintenance respiration rate of the vegetation (g CH_2O m^{-2} d^{-1})

REMOB = remobilization rate of carbohydrates (g CH_2O m^{-2} d^{-1})

TRANS = translocation rate of carbohydrates (g CH_2O m^{-2} d^{-1})

Assimilate partitioning. Assimilate partitioning is the process by which assimilates available for growth are partitioned over leaves, stems, roots, and/or storage organs. It depends on physiological age. Assimilate partitioning pattern in wildcelery is not known. However, the biomass resulting from this process was partitioned for 71.8 percent over leaves, 15.9 percent over stems, and 12.3 percent over roots in two well-developed wildcelery communities in summer (Haller 1974; Titus and Stephens 1983).

Wildcelery exhibits a typical inverse-umbrella shaped depth distribution of shoot biomass from shoot base to tip. In a full-grown, 0.9-m-high wildcelery community in Lake Mendota, Wisconsin, 62 percent of shoot biomass was found within 0.3 m of the sediment/water interface (Titus and Adams 1979a).

In VALLA, assimilate partitioning is used synonymously with biomass partitioning, with the latter following the same distribution pattern as measured in full-grown plants, starting from the time when the shoot tips have reached either the water surface or a vegetation height of 1.2 m.

Shoot biomass is allocated over the vertical axis via a dry matter partitioning coefficient function (DMPC) following the typical inverse-umbrella type shape. Allocation proceeds as follows. First plant biomass is allocated for 18.4 percent

to the three depth layers above the sediment surface and for 11.4 percent to the two layers above these. Allocation to the maximally seven layers above this 0.5 m is equal up to a total plant biomass share of 9.7 percent. When five or less water layers are present, first the lowest water layers are filled according to allocation pattern, and subsequently the remaining plant biomass is added and distributed equally over the found water layers. Roots always contribute 12.3 percent to total plant biomass. Vertical biomass distribution pattern is recalculated and redistributed by VALLA when a rooting depth other than nominal (1.4 m) is chosen.

The following equation describes biomass partitioning over plant organs:

$$GLV = FLV \times GTW$$

$$GRT = FRT \times GTW \qquad (7)$$

$$GST = GST \times GTW$$

where

FLV, FRT, and *FST* are fractions of total dry matter increase allocated to leaves, roots, and stems, respectively (relative)

GLV, GRT, and *GST* are dry matter growth rates of leaves, roots, and stems, respectively (g DW m^{-2} d^{-1})

GTW is dry matter growth rate of the vegetation (plants excluding tubers; g DW m^{-2} d^{-1})

A relational diagram illustrating photosynthesis, respiration, and biomass formation of wildcelery is shown in Figure 4.

Induction and Formation of New Tubers

Tubers are formed just after flowering under relatively short day conditions (<14.7 h) and within a temperature range between 5 and 25 °C. This was concluded by relating published field data from New York and Wisconsin (Titus and Stephens 1983; Donnermeyer 1982) to site daylength and water (or, when not available, average air) temperature conditions of the same year. It is possible that tuber induction in wildcelery is triggered by phytochrome and is associated with increased abscisic acid levels, like in hydrilla (Van, Haller, and Bowes 1978; Klaine and Ward 1984), *Ceratophyllum demersum* (Best 1982), and the terrestrial potato (Kooman 1995). Tubers can only be formed by a plant (not by an already existing tuber). Environmental conditions favoring tuber formation occur in a temperate climate in spring and late summer. Since, in this climate, wildcelery winters by tubers without plants, tubers can only be formed in late summer. However, in other warmer climates where wildcelery may winter by plants and tubers, tuber formation may follow a different timing.

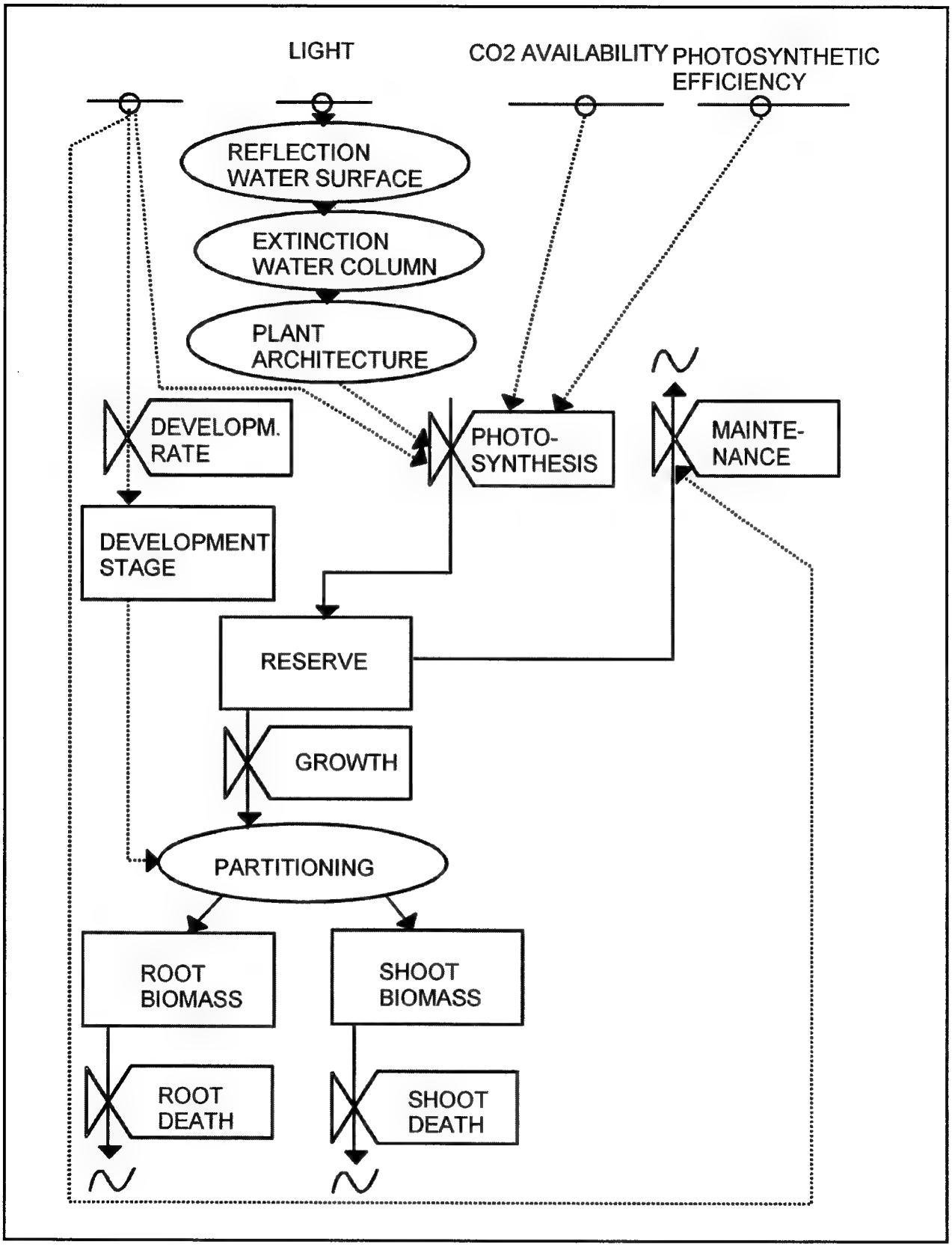


Figure 4. Relational diagram illustrating phososynthesis, respiration, and biomass formation in wildcelery

Tubers grow from assimilates translocated downward from the shoots. Translocation has not been measured in submersed plants. However, estimates based on data pertaining to other plants are: 19 percent of net production in seagrasses (Wetzel and Neckles 1996), 35 percent in Eurasian watermilfoil (Best and Boyd 1996), and approximately 40 percent in hydrilla (Best and Boyd 1996). In terrestrial tuber-producing plants, translocation was 29 percent of net production in cassava (Gijzen 1985) and 35 percent in certain potato varieties (Kooman 1995). The translocated material consisted largely of carbohydrates and was considered as equivalent to starch (Gijzen 1985).

Individual tuber weight and number of tubers concurrently formed by each plant depend on the light level at which the plant grows. Individual tuber weight decreases almost linearly with increasing suspended solids concentration of the water column and, thus, decreasing light level (from 0.102 to <0.01 g dry weight $tuber^{-1}$) parabolically with tuber number concomitantly formed (from 6.5 to 0.5 $plant^{-1}$) (Korschgen, Green, and Kenow 1997), Figure 2. This led us to conclude that wildcelery follows an optmization strategy aimed at forming the largest possible tubers at the light level experienced, possibly because large tubers have a greater survival value than smaller ones. Based on the assumption that the plant follows this optimization strategy, an established plant population growing at a given light level will aim at forming only one tuber weight class, i.e., with an individual tuber weight that allows new plants to survive at that site. Consequently, the differences in tuber weights found in tuber banks can be explained by difference in age between tuber classes, with the oldest class having a lower weight because the tubers have lost weight by senescence, and the youngest class having a lower weight because the tubers were not completely finished before the plants were fully senesced.

In the model, induction of tuber formation occurs at DVS >1.0, daylength <14.7 hr, and in a temperature range of 5 to 25 °C. Once initiated, a tuber class grows from translocated material until a preselected individual tuber weight is reached. Nominal values are 5.5 tubers with a 0.09 g DW individual tuber weight making up a 14.85 g DW critical tuber weight class (*TWCTUB*; $5.5 \times 0.09 \times 30$). Transport of glucose costs dry matter, i.e. 36/38, whereas conversion of starch to glucose increases the dry matter with a factor 10/9. Thus, the total transport 'cost' of downward translocation is a factor $CVT = 1.05$ ($10/9 \times 36/38$). The intensity of translocation is governed by the maximum relative growth rate of the tubers, *RTRL*, that consumes 24.7 percent of net production by the senescing plants, multiplied by *CVT*. This relative growth rate was found by applying the same differential equation as commonly used for simple exponential growth (Thornley and Johnson 1990b; Hunt 1982) to tuber data collected in the field (Titus and Stephens 1983). Thus, a maximum relative growth rate of tubers of 0.247 d^{-1} at a reference temperature of 20 °C was computed. Temperature influences on the relative growth rate of tubers are described in this chapter, section on Wintering and Sprouting of Tuber Bank. Once finished, a tuber class is added to the dormant tuber bank, and the plant starts forming a new tuber class. Tuber initiation continues as long as environmental conditions permit, and tubers are formed as long as the plants can provide assimilates to fill them.

The following equations describe induction and formation of new tubers.

```
IF (REMOB . EQ. 0.0) THEN
    IF (DVS. GT. 1.0. AND. DAYL. LT. 14.7)THEN
        IF (DDTMP .GT. 5.0 .AND. DDTMP .LT. 25.0)THEN
            IF (TGW .GT .0.1) THEN

TRANS = AMAX1 (0., (RTRL * 1./CVT) * (GPHOT – MAINT)))

NNTUB = NPL * NINTUB

TWNTUB = INTGRL (TWNTUB, TRANS, DELT)

IF (TWNTUB .GE. TWCTUB) THEN

NDTUB = NDTUB + (NPL * NINTUB)
```

where

CVT = conversion/transport factor (relative; -)

DAYL = daylength (h)

DDTMP = daily average daytime temperature (°C)

DVS = development rate of the plant (-)

GPHOT = daily total gross assimilation rate of the community (g CH_2O m^{-2} d^{-1})

MAINT = maintenance respiration of the vegetation (g CH_2O m^{-2} d^{-1})

NDTUB = dormant tuber number (dormant tubers m^{-2})

NINTUB = tuber number concurrently initiated per plant (conc. initiated tubers $plant^{-1}$)

NNTUB = new tuber number (new tubers m^{-2})

NPL = plant density (plants m^{-2})

REMOB = remobilization rate of carbohydrates (g DW m^{-2} d^{-1})

RTRL = relative tuber growth rate at ambient temperature (g DW $tuber^{-1}$ d^{-1})

TGW = total live plant dry weight, excluding tubers (g DW m^{-2})

TRANS = translocation rate (g CH_2O m^{-2} d^{-1})

TWCTUB = total critical dry weight of new tubers (g DW m^{-2})

TWNTUB = total dry weight of new tubers (g DW m^{-2})

Flowering and Senescence

The occurrence of flowering affects subsequent metabolic activity of the vegetation. The timing of flowering is, therefore, extremely important for the physiological activity and biomass formation, while the actual investment of dry matter in flowers and seeds proves to be only minor (Donnermeyer 1982; Titus and Stephens 1983). After flowering, senescence sets in resulting in loss of particulate plant material, while a considerable part of net production is translocated downward to the tubers with the remainder of net production being allocated following the typical pattern described in this chapter in subsection "Maintenance, Growth, and Assimilate Partitioning."

Senescence refers to the loss of capacity to carry out essential physiological processes and to the loss of biomass. The fundamental processes involve physiological aging and protein (enzyme) breakdown. These processes are difficult to quantify. It is known that hormones are important messengers in this context, but not how they precisely act. High temperature usually accelerates senescence.

In VALLA, the timing and value of relative death rate (RDR) of the plants have been derived from field observations on plant biomass in Chenango Lake, New York (Titus and Stephens 1983). A mechanistic approach to senescence has been chosen by setting the death rate at a certain fraction of plant biomass lost per day once the conditions for growth deteriorate. The timing of onset of senescence was found by running the model repeatedly with different development rates, base, and reference temperatures until a good fit between simulated and measured values was accomplished. Thus, initiation of senescence for plants was set at DVS 2.001. The value for the relative death rate of the plants was found by applying the same differential equation as commonly used for simple exponential growth, to describe exponential decrease in biomass after flowering, with a negative specific decrease rate. Thus, RDR's of 0.009 and 0.021 d^{-1} were computed for the period directly following maximum plant biomass and the subsequent period, respectively. The latter, highest RDR of 0.021 d^{-1} was used in the model. It is presumed to increase with temperature between 20 and 50 °C through a relative temperature function. This function describes processes relative to a reference temperature of 20 °C at which the function has the value of 1, to increase with a Q_{10} of 2 at temperatures between 20 and 40 °C, and to increase further to the value of 1 at 50 °C.

A relational diagram illustrating translocation and senescence is shown in Figure 5.

Choice of Parameter Values

A relatively simple simulation model like VALLA includes parameter values that can be defined with varying certainty. Most parameters have been calculated/estimated from published literature (Table 2). Only development rate in relation to 3 ^{0}C day-degree sum and base temperature have been calibrated by running the model. The choice of parameter values has been detailed in the preceding sections of this chapter.

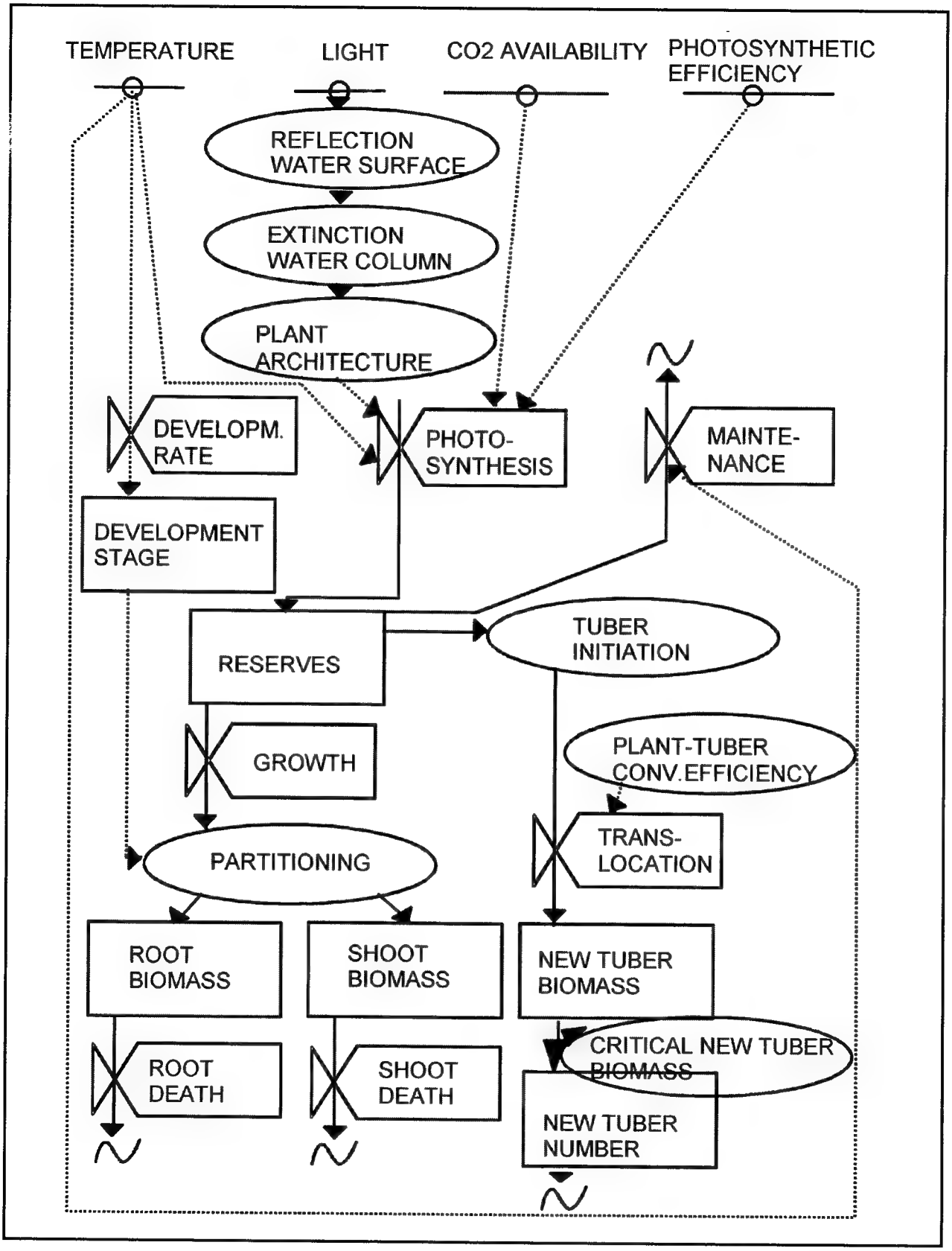


Figure 5. Relational diagram illustrating translocation and senescence following anthesis in wildcelery

Table 2
Parameter Values Used in VALLA

Parameter	Abbreviation	Value	Reference
Morphology, phenological cycle, and development			
First Julian day number	DAYEM	1	
Base temperature for juvenile plant growth	TBASE	3°C	Calibrated
Development rate as function of temperature	DVRVT* DVRRT	0.015 0.040	Calibrated
Fraction of total dry matter increase allocated to leaves	FLVT	0.718	1, 2
Fraction of total dry matter increase allocated to stems	FSTT	0.159	1, 2
Fraction of total dry matter increase allocated to roots	FRTT	0.123	1, 2
Maximum biomass and plant density			
Maximum biomass		496 g DW m^{-1}	2
Plant density	NPL	30 m^{-2}	1
Wintering and sprouting of tuber bank			
Initial tuber density	NT	233 m^{-2}	1
Initial weight per tuber	INTUB	0.090 g DW. $tuber^{-1}$	3, 4
Relative tuber death rate (on number basis)	RDTU	0.018 d^{-1}	1
Initial growth of sprouts			
Relative conversion rate of tuber into plant material	ROC	0.0576 g CH_2O g DW^{-1} d^{-1}	5
Relation coefficient tuber weight-stem length	RCSHST	12 m. g DW^{-1}	5, 6
Critical shoot weight per depth layer	CRIFAC	0.0091g DW 0.1 m plant $layer^{-1}$	3, 4
Survival period for sprouts without net photosynthesis	SURPER	23 d	7,8
Light, photosynthesis, maintenance, growth, and assimilate partitioning			
Water type specific light extinction coefficient	L	0.43-0.80 m^{-1}	1
Plant species specific light extinction coefficient	K	0.0235m^2 g DW^{-1}	9
Potential CO_2 assimilation rate at light saturation for shoots	AMX	0.0165 g CO_2 g DW^{-1} h^{-1}	9
Initial light use efficiency for shoots	EE	0.000011 g CO_2 J^{-1}	10
Reduction factor for AMX to account for senescence plant parts	REDF	1.0	User def.
Daytime temperature effect on AMX as function of DVS	AMTMPT*	0 – 1	
Reduction factor to relate AMX to water pH	REDAM	1.0	
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	10
Dry matter allocation to each plant layer	DMPC*	0-1	9
Thickness per plant layer	TL	0.1 m	11
Water depth	DEPTH	1.4 m	User def.
Daily water temperature (field site)	WTMPT	-, °C	User def.
Total live dry weight measured (field site)	TGWMT	-, g DM m^{-2}	User def.
Induction and formation of new tubers			
Translocation (part of net photosynthetic rate)	RTR	0.247	4, 12,13
Tuber number concurrently initiated per plant	NINTUB	5.5 $plant^{-1}$	13
Critical tuber weight	TWCTUB	14.85 g DW m^{-2}	1, 3,13
Tuber density measured (field site)	NTMT	233 m^{-2}	1
Flowering and Senescence			
Relative death rate of leaves (on DW basis; Q10 =2)	RDRT	0.021 d^{-1}	1
Relative death rate of stems and roots (on DW basis; Q10=2)	RDST	0.021 d^{-1}	1
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	User def.

Notes: (1) Titus and Stephens 1983; (2) Haller 1974; (3) Korschgen and Green 1988; (4) Korschgen, Green, and Kenow 1997; (5) Bowes, Holaday, and Haller 1979; (6) Best and Boyd 1996; (7) Titus and Adams 1979b; (8) E. P. H. Best, unpubl. 1987; (9) Titus and Adams 1979a; (10) Penning de Vries and Van Laar 1982a,b; (11) Titus et al. 1975; (12) Donnermeyer 1982; (13) Donnermeyer and Smart 1985.
* Calibration function.

4 Performance Tests

Simulated and Measured Behavior of a Wildcelery Community in Chenango Lake, New York

Nominal run

The seasonal changes in biomass of plant shoots and roots, and of the tuber bank as simulated by VALLA are shown in Figure 6. Simulated plant biomass compared well with average plant biomass measured in Chenango Lake, New York (Titus and Stephens 1983). Plant biomass reached its maximum at the same time, and peak biomass was somewhat higher in the simulated than in the measured plant community, notably 56.1 versus 50.1 g DW m^{-2}. However, the latter may be due to the relatively large tuber size/concurrently initiated tuber number combination (0.09 g DW $tuber^{-1}$, 5.5 $tubers\ plant^{-1}$) used to initiate this nominal run. Measured tuber size was 0.055 g DW $tuber^{-1}$, and another model run starting with the measured tuber size generated a peak biomass of 48 g DW m^{-2}. Moreover, one exceptionally high plant biomass value measured in the same lake was 85 g DW m^{-2}.

Simulated transport of carbohydrates was substantial in the beginning of the growth season when upward carbohydrate remobilization from the tubers supports initial sprouting, but far higher after flowering when downward carbohydrate translocation from plant organs supports the filling of the tubers (Figure 7). Carbohydrate transport could be in the same range as net assimilation at the beginning and end of the growth season (Figures 7 and 8). Maintenance respiration was usually considerably lower than assimilation but could be in the same range of translocation just after flowering (Figure 8).

Running the model with (24-hr average) air temperatures with a lag period of 1 day instead of running the model with measured water temperatures as forcing variables yielded higher assimilation (Figure 9) and plant biomass values than found in the nominal case. This can be explained by the fact that water temperatures in the lake were relatively low compared to air temperatures, because of the large inflow of groundwater (Titus and Stephens 1983). In our experience, a lag period of 7 days between model daily air and measured temperatures usually describes this relationship well for shallow, up to 5 to 6 m deep, water bodies without large inflows of groundwater. It has to be cautioned that the relationship between the temperatures of air and water body may differ, since temperatures within each water body are influenced by catchment morphometry, wind speed,

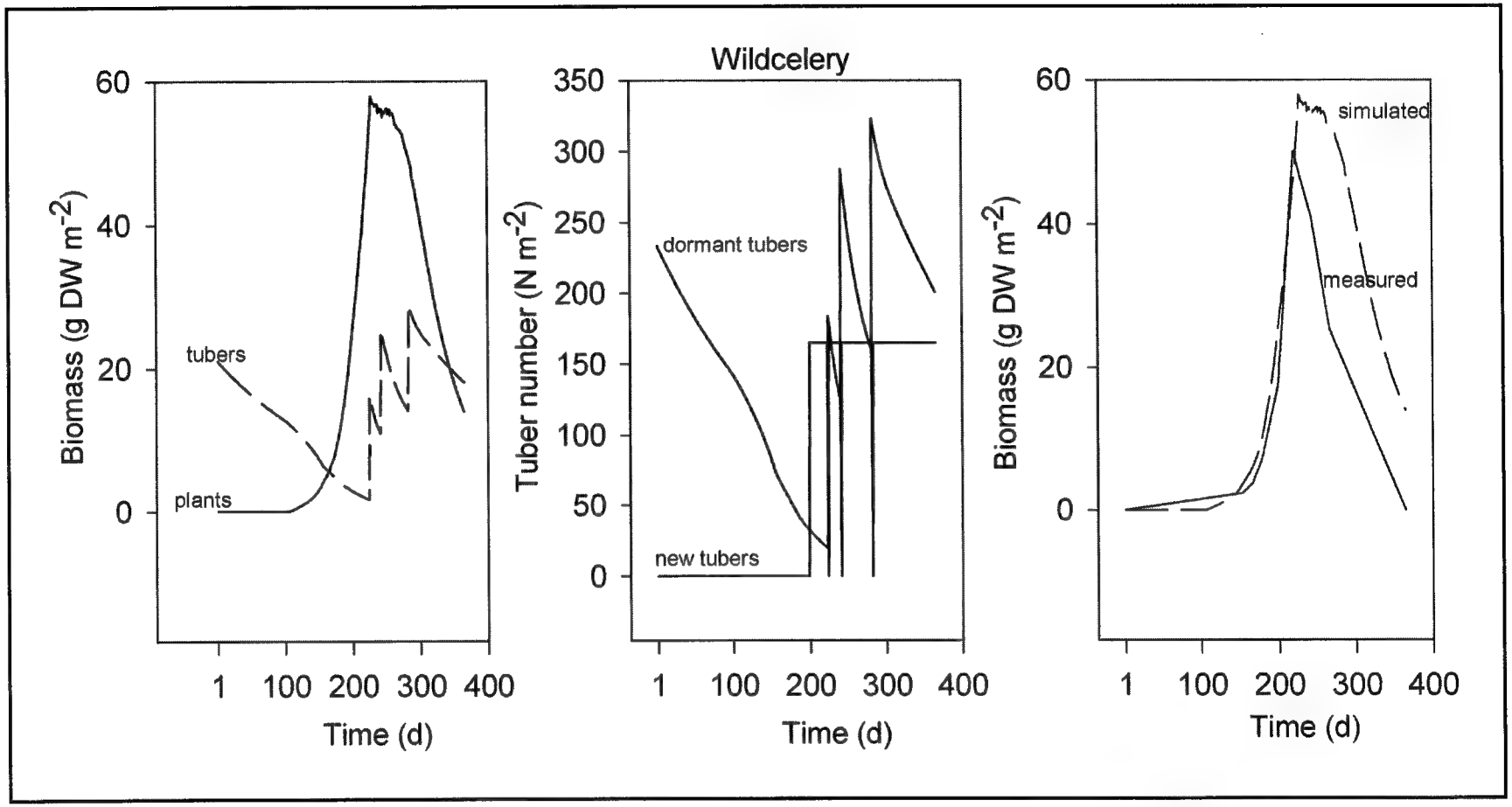


Figure 6. Simulated biomass of plants, dormant and new tuber numbers, and measured plant biomass of a wildcelery community in Chenango Lake, New York. Nominal run. Field data from Titus and Stephens (1983); climatological data 1987, Binghamton, New York (longitude 75° 50' E, latitude 42° 15' N); water depth 1.4 m; light extinction coefficient 0.43 m^{-1}

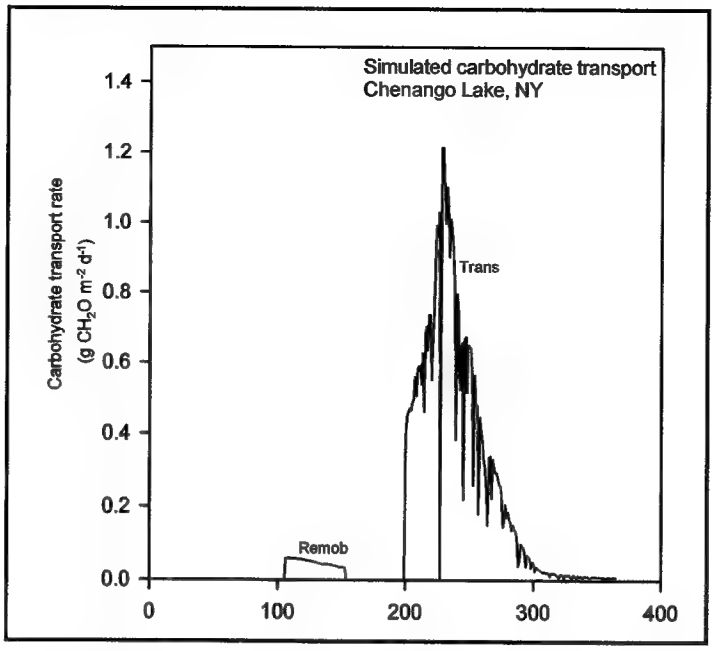


Figure 7. Simulated behavior of carbohydrate flow through plant compartments of a wildcelery community in Chenango Lake, New York (Carbohydrate remobilization and upward transport from the tubers is used for initial growth of plants. Downward carbohydrate translocation into tubers occurs during anthesis and senescence (Initial biomass and climatological data as in nominal run))

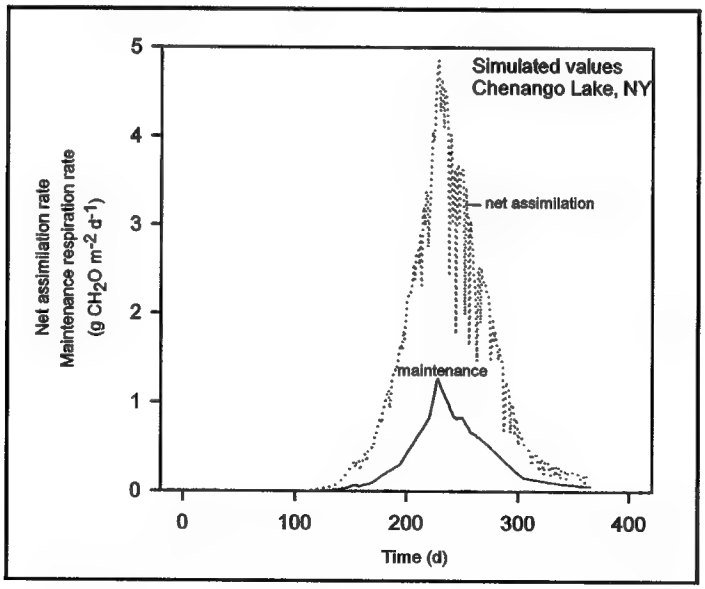


Figure 8. Simulated rates of daily net assimilation and maintenance respiration of a wildcelery community in Chenango Lake, New York (Initial plant parameter values as in nominal run)

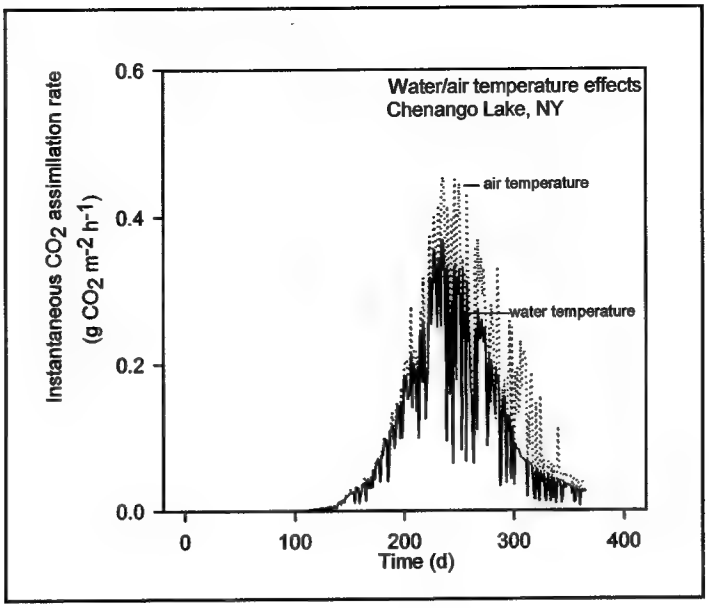


Figure 9. Simulated photosynthetic rates of a wildcelery community in Chenango Lake, New York, with water or air temperatures as input (Initial plant parameter values as in nominal run)

fetch, mixing processes, and upward seepage. This example illustrates the usefulness of inclusion of both temperature options in the model, facilitating its operation by users who do not possess a full data set of water temperatures for the water body for which they desire to run the model.

Running the model for the same lake and year, but with both plants and tubers initially present, showed that peak plant biomass was greatly increased and more tuber classes were finished (4 instead of 3 in the nominal case; Figure 10B). This large difference in peak biomass is due to the ability of the plant community to fully capture the high spring irradiance at this latitude of 43° N, which they cannot without wintering shoots. Thus, wintering shoots would provide a distinct advantage for this plant species. However, wintering shoots have only been reported to occur in a tropical climate. A simulation started from the measured tuber size/chosen concurrently initiated tuber number combination yielded peak plant biomass that was almost equal in simulated and measured plant community (Figure 10C; Figure 6), and the simulated tuber numbers were within the range found in a wildcelery community in the same lake (Titus and Stephens 1983).

Effects of differences in leaf surface: dry weight ratio

A large range of leaf surface area: dry weight ratios (K-value) in wildcelery have been published. It appears that even two K-values may pertain to the same plant community, i.e., a K-value of 0.0235 m^2 g DW^{-1} to a well-developed monotypic stand in situ and of 0.013-0.019 m^2 g DW^{-1} to wildcelery plant material (removed from its community-specific spatial distribution) in the laboratory. All these K-values were measured in wildcelery originating from Lake Mendota,

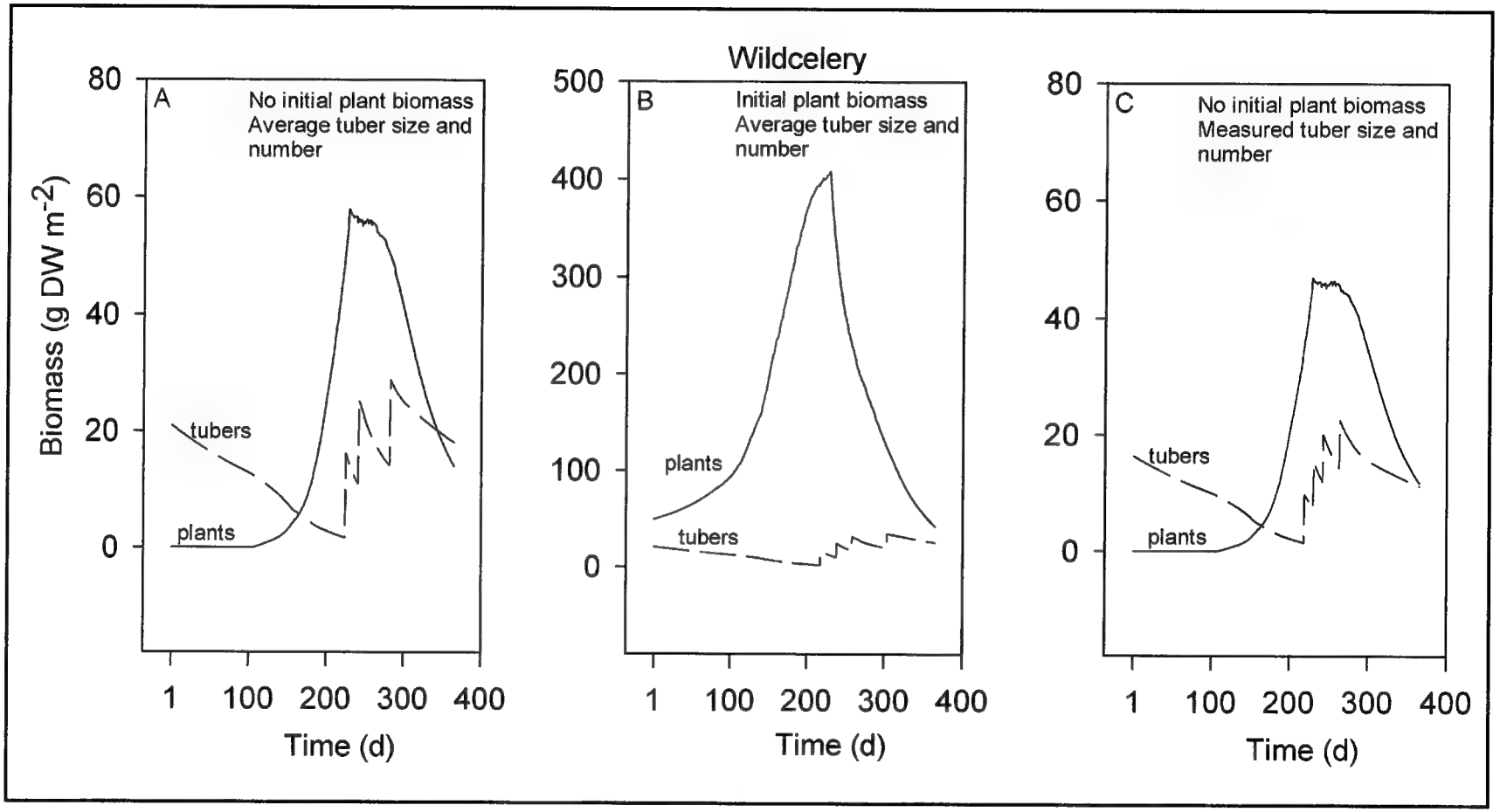


Figure 10. Simulated biomass of plants and tubers of a wildcelery community in Chenango Lake, New York, started from different initial biomass conditions, but run in the same environmental and climatological, nominal conditions. (A) Plant biomass); tuber size 0.09 g DW; tuber bank 233 m^{-2}; (B) Plant biomass 50 g DW m^{-2}tuber size 0.09 g DW; tuber bank density 233 $m^{-2;}$(C) Plant biomass 0; tuber size 0.055 g DW; tuber bank density 233 m^{-2}

Wisconsin; longitude 89° 20' W, latitude 43° 08' N. Other K-values, measured in warmer climates but not in the tropics, were either in the same range (0.018 m^2 g DW^{-1}; Lake Biwa, Japan; longitude 136° E, latitude 35° 30' N (Ikusima 1970)) or far lower (0.0051 m^2 g DW^{-1}; longitude 139° E, 35° 0' S (Blanch, Ganf, and Walker 1998)).

Simulations indicated that peak plant biomass decreased with decreasing K-value but not proportionally (Figure 11). A wildcelery community starting from the same tuber bank as the nominal one and characterized by a K-value of 0.0051m^2 g DW^{-1} (measured in Australian wildcelery plant material) would produce only about 30 percent of the biomass of a community with a nominal K-value. Running the model from the same tuber bank for a community with a K-value of 0.0051m^2 g DW^{-1} under tropical climatological conditions (Tampa, Florida; longitude 82° 32' E, latitude 27° 58' N; average 1975 to 94) indicated that in these conditions somewhat more plant material would be produced, but no tubers, with a far lower simulated peak biomass than found. Running the model from an initial plant biomass of 50 g DW m^{-2} (wildcelery plants can be present year-round) and tuber bank under tropical conditions indicated that in this case a far higher peak biomass can be produced, i.e., approximately 500 g DW m^{-2} and that two tuber classes can be finished. Thus, in wildcelery lower K-values may also be associated with warmer climates just as in Eurasian watermilfoil (Best and Boyd 1999a).

Effects of differences in tuber size and number

Wildcelery has shown a tendency to limit its distribution to the most shallow parts of its areal in the Upper Mississippi River pools, where it used to be widespread and to produce relatively smaller tubers than formerly.

To investigate the importance of tuber size for survival of a wildcelery community in temperate conditions, the model was run with a different tuber size/concurrently initiated tuber number combinations under nominal conditions. Reducing the tuber size to 0.04 g DW $tuber^{-1}$ concomitant with a concurrently initiated tuber number of 2.5 $plant^{-1}$ (Figure 2) reduced peak biomass by a factor of 2, but increased the number of finished tuber classes from three to seven (Figure 12A). The predominant tuber size measured under nominal conditions was somewhat larger, i.e., 0.055 g DW $tuber^{-1}$ (Titus and Stephens 1983). However, running the model with the same initial conditions but for a greater depth (2.5 instead of 1.4 m), indicated that in the latter case plant biomass is greatly reduced and only three small-sized tuber classes are produced (Figure 12B). Running the model at the same depth of 2.5 m and with the same tuber size/concurrently initiated tuber number, but starting from a tuber bank density of 60 m^{-2}/size 0.04 g DW $tuber^{-1}$, that represents the situation at the end of the former simulation, indicated that this wildcelery community would not be viable (Figure 12C). This lack of viability can be explained by the low density of the tuber bank, allowing only one plant cohort to sprout. Since this plant cohort is not able to reach a self-supporting situation within the water column early in the season because of the relatively large water depth and low irradiance, it dies. However, the plant cohort could survive at a shallower water depth.

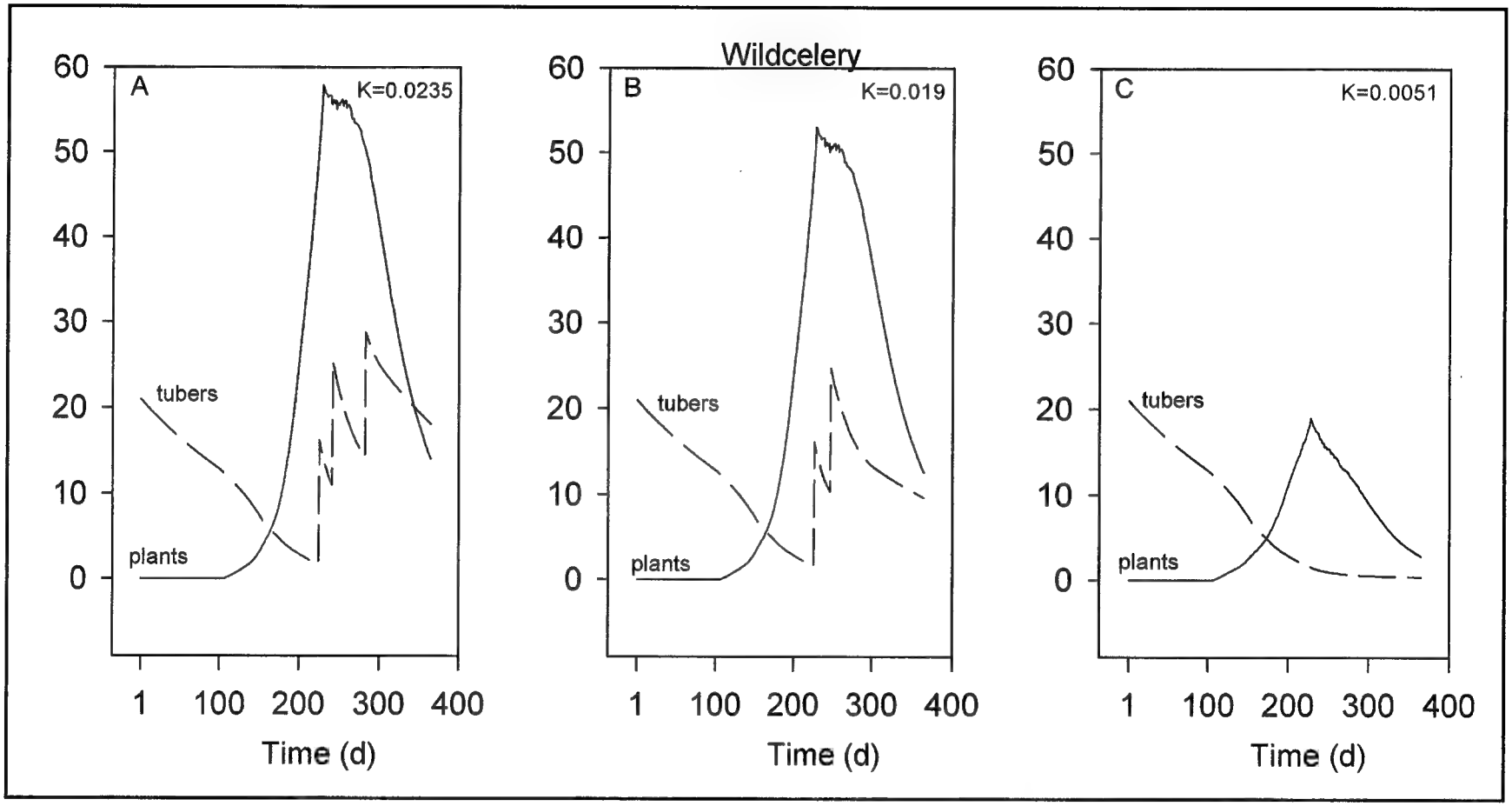


Figure 11. Simulated biomass of plants and tubers of a wildcelery community in Chenango Lake, New York, started from identical nominal initial biomass conditions, except for the K-value (Climatoligical data as in nomihal run). K-values of (A) 0.0235 m2 g DW^{-1} (Titus and Adams 1979b); (B) 0.019 m2 g DW (Titus and Adams 1979b); (C) 0.0051 m^2 g DW^{-1} (Blanch, Ganf, and Walker 1998)

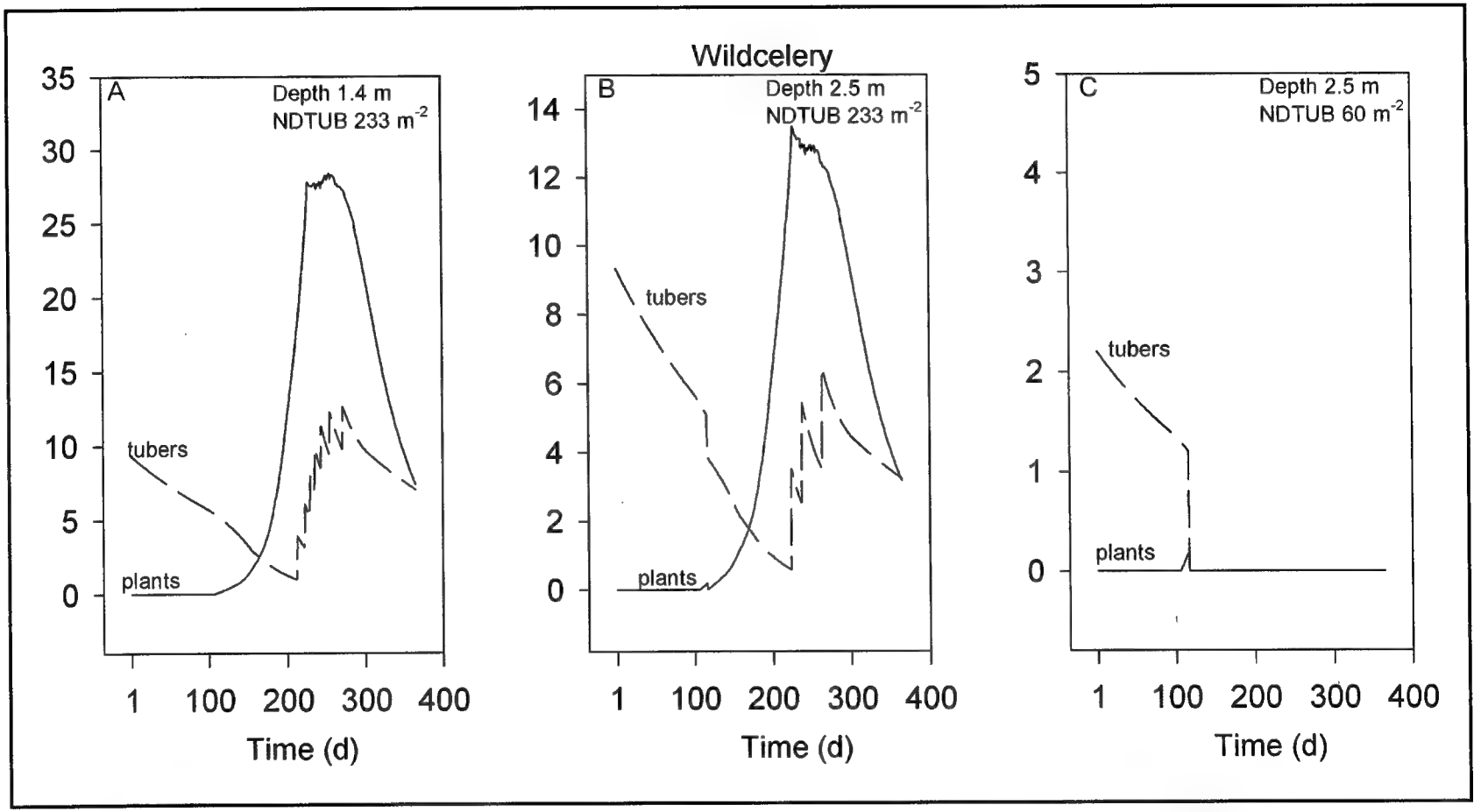


Figure 12. Simulated biomass of plants and tubers of a wildcelery community in Chenango Lake, New York, started from nominal initial biomass data differeing in tuber size, tuber bank density, and rooting depth (Climatological data as in nominal run). (A) Tuber size 0.09 g DW, tuber bank density 233 m^{-2}; rooting depth 1.4 m; (B) Tuber size 0.09 g DW, tuber bank density 233 m^{-2}; rooting depth 2.5 m; (C) Tuber size 0.055 g DW, tuber bank density 60 m^{-2} rooting depth 2.5 m.

Simulated and Measured Behavior of a Wildcelery Community at Other Latitudes

To investigate whether the model could simulate behavior of a wildcelery community at other sites besides the nominal one, runs were made for two other sites, one more western, i.e., Lake Mendota, Wisconsin, and another, tropical and more south, i.e., ponds at Fort Lauderdale, Florida.

A simulation was performed of a wildcelery community in Lake Mendota, Wisconsin, starting from site-specific community, water depth, water transparency, and climatological data. Plant community-specific data included: initial plant biomass absent, tuber size 0.03 g DW, concurrently initiated tuber number 1.5 $plant^{-1}$, and tuber bank density of 233 m^{-2}. Site-specific environmental data included: 1.2-m water depth and 0.7-m^{-1} light extinction coefficient. In these conditions, simulated plant biomass remained low, maximally 25 g DW m^{-2}, and no tuber classes were finished. Because the simulated maximum plant biomass was far lower than published (average peak biomass 344, and minimum 266 g DW m^{-2} (Titus and Adams 1979a)), and wildcelery populations in Lake Mendota have been described as stable, several other simulations were done to explore community- and site-specific characteristics favoring such a sustainable population. Increasing the tuber size from 0.03 to 0.09 g DW increased peak biomass from 25 to 105 g DW m^{-2} and the number of finished tuber classes to five. Increasing water transparency by decreasing the light extinction coefficient from 0.7 to 0.4 m^{-1} increased peak biomass from 25 to 130 g DW m^{-2} and the number of finished tuber classes to seven. Introduction of the largest tuber size published, 0.11 g DW, again increased peak biomass to 150 g DW m^{-2} but allowed only five tuber classes to be finished. Even in very clear water (extinction coefficient 0.4 m^{-1}), a very shallow, 0.2-m water depth, and with the most profitable tuber size, wildcelery would only produce maximally 195 g DW m^{-2} in Lake Mendota (Figure 13). The latter result led us to believe that the high plant biomass range of 266 to 344 g DW m^{-2} published by Titus and Adams (1979a) is an overestimate, or that spring growth starts partly from wintering shoots.

A simulation was performed of a wildcelery community in earthen ponds near Fort Lauderdale, Florida, starting from site-specific community, water depth, water transparency, and climatological data. Plant community-specific data included: initial plant biomass 50 g DW m^{-2}, tuber size 0.09 g DW, concurrently initiated tuber number 5.5 $plant^{-1}$, tuber bank density 233 m^{-2}. Site-specific environmental data included: 1.5-m water depth and 0.4-m^{-1} light extinction coefficient. In these conditions, simulated plant biomass was high, maximally 403 g DW m^{-2}, and three tuber classes were finished at the very end of the year. Tuber weights and numbers of the Fort Lauderdale community were not published, so comparison between simulated and measured tuber data is not possible. Simulated maximum plant biomass in this case was within the measured peak biomass range of 298 to 496 g DW m^{-2} (Figure 13C). It was enhanced to 450 g DW m^{-2} by decreasing the K-value from 0.0235 to 0.019 m^2 g DW^{-1}, and even surpassed the maximum measured value by decreasing the K-value further to 0.0051 m^2 g DW^{-1}.

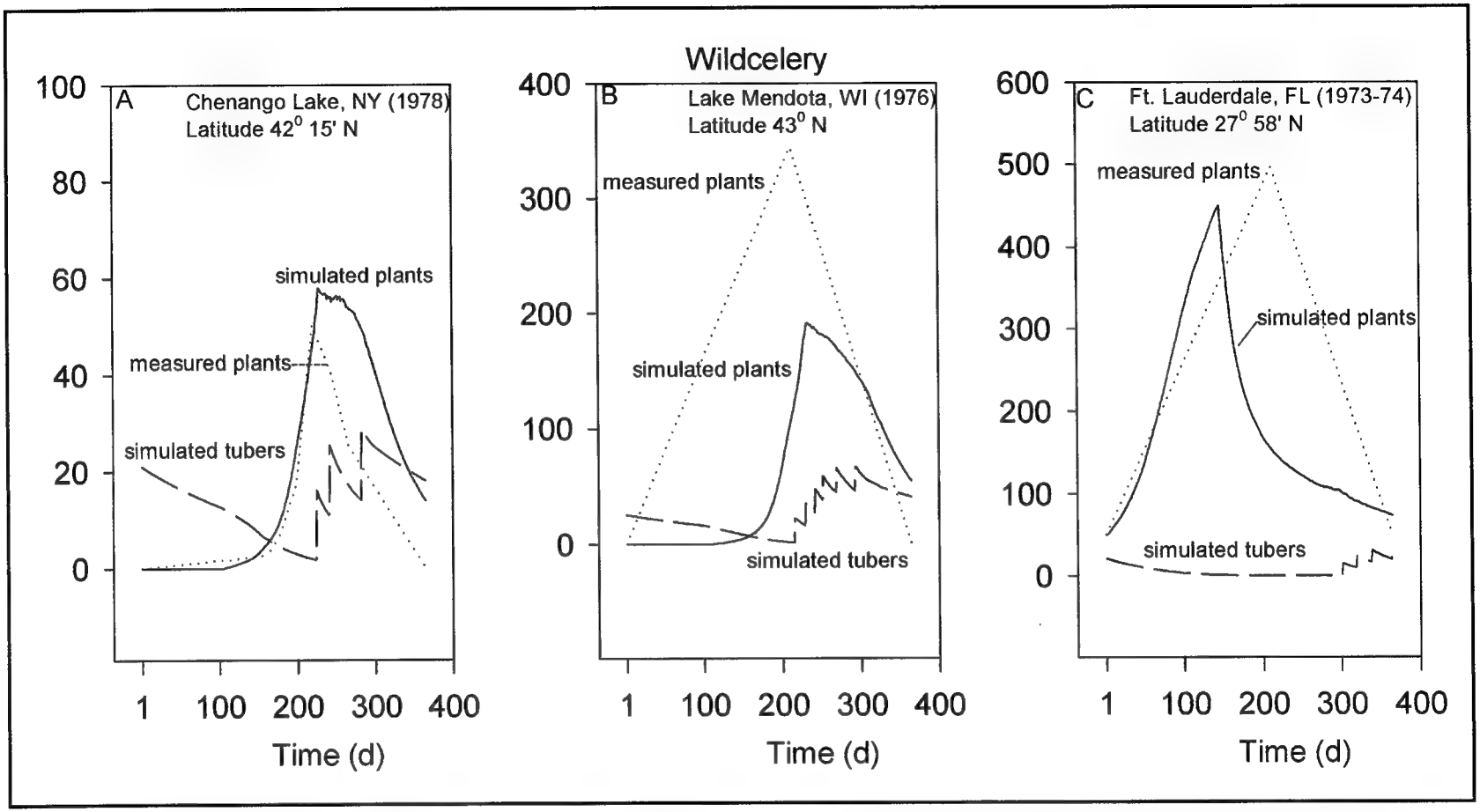


Figure 13. Simulated biomass of plants and tubers of a wildcelery community at sites differing in latitude. (A) Chenango Lake, New York (longitude 75° 50' E, latitude 42° 15' N; tuber size 0.09 g DW, tuber bank density 233 m^{-2}; water depth 1.4 m; light extinction coefficient 0.43 m^{-1}; climatological data 1987; validation data 1978 (Titus and Stephens 1983)). (B) Lake Mendota, Wisconsin (longitude 89° 20' E, latitude 43° 08' N; tuber size 0.11 g DW, tuber bank density 233 m^{-2}; water depth 0.2 m; light extinction coefficient 0.4 m^{-1};climatological data 1971-75; validation data 1976 (Titus and Adams 1979a)). (C) Fort Lauderdale ponds, Florida (longitude 82° 32' E, latitude 27° 58' N; plant biomass 50 g DW m^{-2}; tuber size 0.09 g DW, tuber bank density 233 m^{-2}; K-value 0.018 m^2 g DW^{-1}; water depth 1.5 m; light extinction coefficient 0.4 m^{-1}; climatological data 1975-84; validation data 1973-74 (Haller 1974)).

Comparison of biomass produced in the various climatological conditions (Figure 13) indicates that in a temperate climate generally less biomass is produced and investment in vegetative reproduction is relatively higher than in a tropical climate. This example illustrates the usefulness of inclusion of phenology tied to degree-day sum in the model, allowing it to perform simulations for different sites and climates facilitating its operation by users who do not possess a full plant characteristics and environmental data set for the water body for which they desire to run the model.

The tentative difference in importance of sexual reproduction between climates can not be explored with the current version of the model, since sexual reproduction has not been included.

Historical and Simulated Behavior of a Wildcelery Community in a Riverine Environment Subject to Flooding

Wildcelery is an important riverine macrophyte that provides food and habitat resources for waterfowl, fishes, and invertebrates in the Upper Mississippi River (UMR). Navigation pools along the Mississippi Flyway have historically been used by migrating waterfowl as staging areas in part because of abundant populations of wildcelery (Bellrose et al. 1983; Korschgen and Green 1988). Recent declines in these populations have caused concern and have been attributed to eutrophication, competition by other macrophytes such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) and American lotus (*Nelumbo lutea* (Willd.) Pers.), drought, and flooding. It is desirable to improve management programs aimed at enhancing wildcelery populations, but these programs require an improved understanding of the population dynamics of wildcelery and factors affecting these.

Detailed biomass dynamics of wildcelery have been recorded in the early 1980's, when populations were still substantial (Pool 9, Donnermeyer 1982). Subsequently, wildcelery populations have been included in regular surveys of several navigation pools, but only by species presence or absence, not characterized by plant and tuber biomass.

Simulations were carried out to evaluate the effects of daily changes in water level during different hydrological years on a typical wildcelery community in Pool 8 of the UMR. Stage data collected at the dam of Pool 8 were used to document water level fluctuations over a 10-year period, i.e., from 1985 to 1994. In this period, 1985 is considered as a normal hydrological year, 1986 a normal flood year with floods in spring and autumn, 1993 an abnormal flood year with one flood in summer, and 1986 a drought year (Figure 14). Disappearance of large portions of wildcelery populations in 1993 and 1988 have been observed (Rogers 1994; Spink and Rogers 1996). The simulations were done starting from a nominal wildcelery community, site-specific environmental data, and site- and year-specific climatological data. Site-specific environmental data included: water depth daily varying as would be experienced by a community at 0.5-m rooting depth; light extinction coefficient ranging from 2.619 to 3.173 m^{-1} during

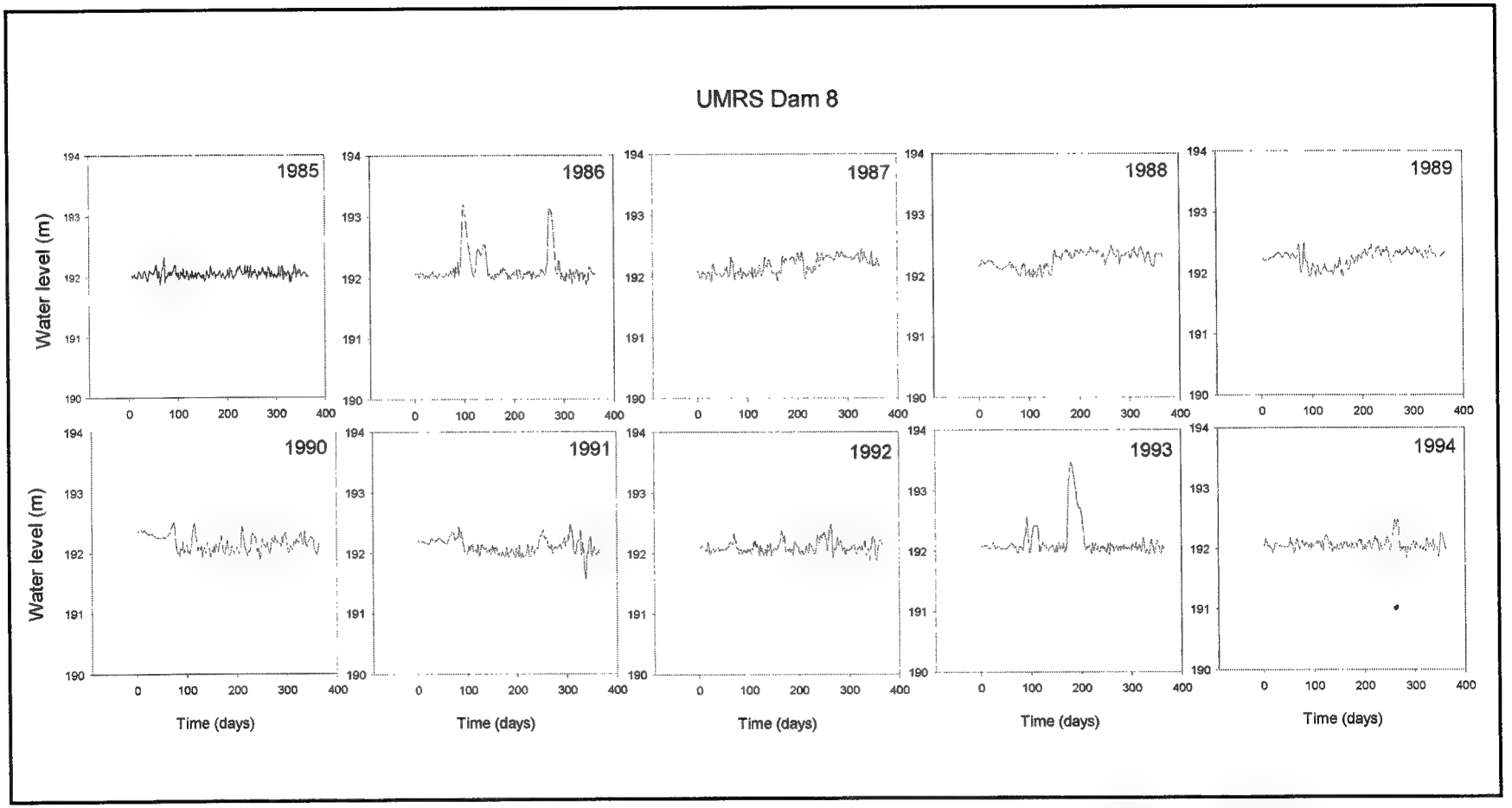


Figure 14. Water level fluctuations over a 10-year period measured at the dam of Pool 8 of the Upper Mississippi River, Wisconsin (data by J. H. Wlosinski, U.S. Geological Survey, La Crosse, WI). Flat pool is considered to be the average summer (June, July, August) value during normal hydrological years over the 1985-94 period; abnormal hydrological years were: 1986, 1988, and 1993

the period of May to October, and set to 2.0 m^{-1} the rest of the year (converted via Giessens relationship from Secchi disk readings, (Giessen, Van Katwijk, and Den Hartog 1990), correlated with 10-year data on total suspended solids concentrations). Historical data indicate that in 1980 plant biomass peaked in mid-August at 217 g DW m^{-2} and tuber biomass was low (maximally 14-16 g DW m^{-2} (Donnermeyer 1982); Figure 15A).

Running VALLA with nominal initial plant biomass and tuber bank data at a constant 1.1-m water depth (annual average in the historical nine-point dataset) with a 10-year average climate, indicated that a peak biomass of only 60 g DW m^{-2} was formed, but no tubers. Water fluctuations in 1980 were substantial. In this case, the average annual water depth derived from the nine measured values may have exceeded the water depth experienced by the plant community during the growth season, and therefore, the simulated plant biomass was lower than measured. The next simulation, at a constant, shallower 0.5-m water depth, indicated that in this case more biomass was produced and that two tuber classes were finished (Figure 15B). Surprisingly, far more biomass could be produced and five tuber classes were finished under a normal water level fluctuation regime in Pool 8 pointing to a tentative positive influence of relatively small water level fluctuations (Figure 15C). Normal flooding inhibited biomass and tuber production somewhat, allowing only four tuber classes to be finished but the population to persist (Figure 15D). The relatively small size of this effect was attributed to the fortuitous timing of the high water levels that occurred only in spring and autumn, still allowing the plants to fully benefit from the high summer irradiance at normal water levels. Abnormal flooding, however, reduced the finished number of tuber classes by a factor of >2 in the 0.5-m-depth class (Figure 15E) and completely prevented tuber formation in the 1-m-depth class. The harshness of this effect was attributed to the fact that the plants could not fully benefit from the high summer irradiance because of the high summer water levels. The effect of the 1988 drought was most surprising and detrimental. In this year, substantial plant biomass could be produced peaking relatively early in the growth season. However, tuber formation was severely inhibited because (a) water levels were kept relatively high later in summer, possibly as a water conservation measure, causing increased extinction of light within the water column, and (b) temperatures were relatively high, causing increased respiration and senescence. The increased light extinction in the water column may even have been larger in situ than in the simulation, since during droughts not only water levels may change but also extinction within the water column increases by stimulation of algal blooms. The seasonal changes in the light extinction coefficient were kept the same in all simulations.

This example illustrates how relatively low- and high-frequency fluctuations in water levels might affect submersed plant populations, without even taking plant-specific adaptation characteristics into consideration. Ability of plants to adapt to changes in water level may be an important characteristic for their persistence in rivers, reservoirs, and estuaries. Although this ability is a rather intensively discussed research topic, pertinent ecological data are currently largely lacking.

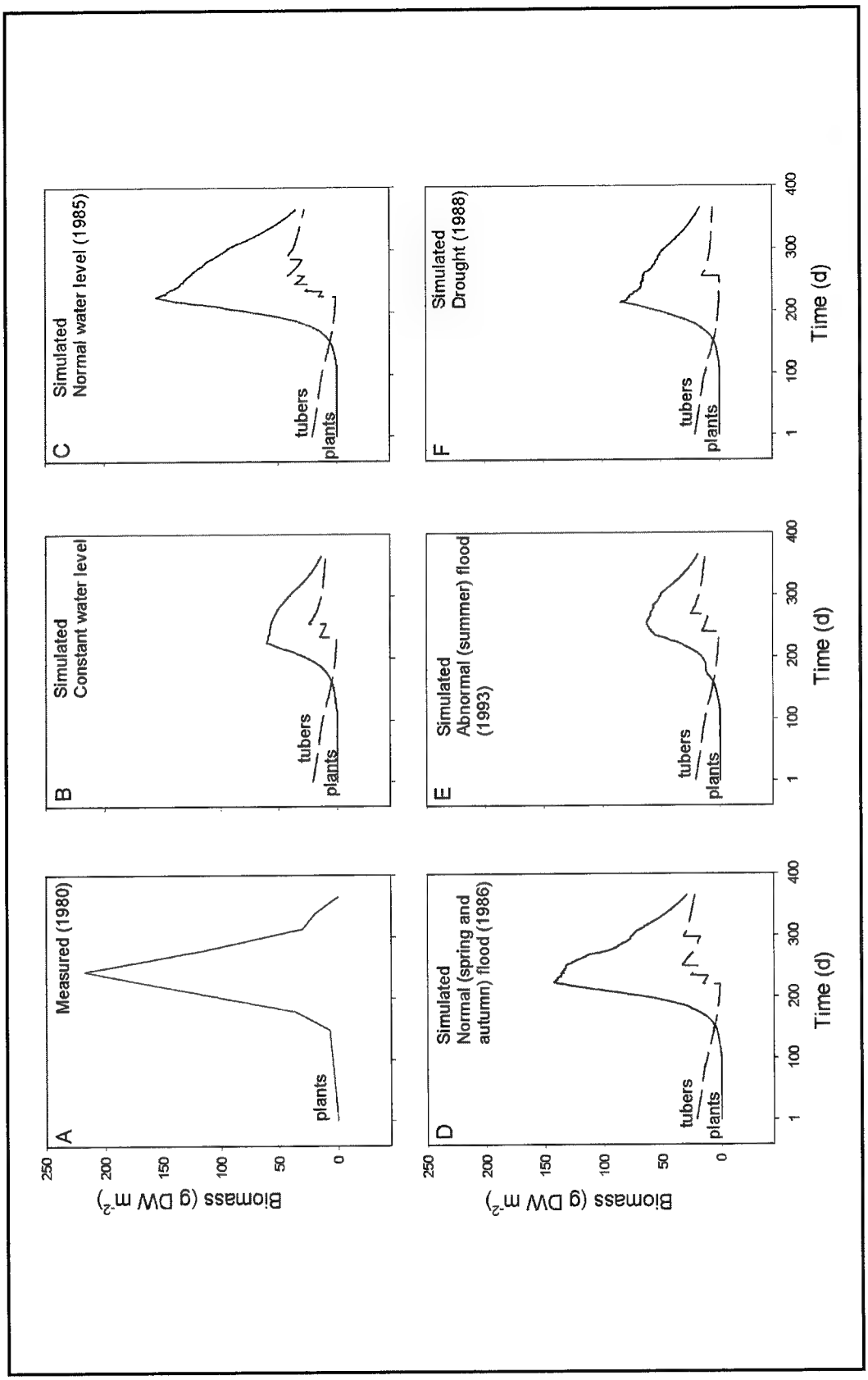


Figure 15. Comparison of historical and simulated data on biomass of plants and tubers of wildcelery in the Upper Mississippi River. (A) Historical data: measured plant data Pool 9, 1980, average water depth 1.1 m (longitude 91° 30' W, latitude 43° 10' N; Donnermeyer 1982). Simulations: Nominal initial biomass data; light extinction coefficients derived from 10-yr average background total suspended solids values measured in the nearby Pool 4 in the 1980's (Bartell et al. 2000); climatological data, Minnesota/St. Paul, Wisconsin (longitude 93° W, latitude 45° N). (B) Water level, annual average historical dataset; climate average 1985-94; (C) Water level, daily values 0.5-m-depth class; climate 1985; (D) Water level, daily values 0.5-m-depth class; climate 1986; (E) Water level: daily values 0.5-m-depth class; climate 1993; (F) Water level, daily values 0.5-m-depth class; climate, 1986.

Simulated Behavior of a Wildcelery Community Subject to Biomass Removal; Effects of Cutting and Grazing

Effects of man-made control activities, like cutting at different times and at various water depths, can be calculated also using Table 6 of VALLA (version 1.0). Thus, in the latter case the model can be used as a tool for aquatic plant and lake management agencies (Table 3, herein).

Table 3
Effects of Cutting Date and Depth on Maximum Shoot Biomass and End-of-Year Tuber Number (Results were obtained in a 1-year simulation under Ft. Lauderdale, Florida, average 1975-84 conditions, starting without and with 50 g DW m^{-2} plant biomass, 0.09 g DW initial tuber size, a tuber bank density of 233 m^{-2}; K-value 0.018 m^2 g DW^{-1}; water depth 1.5 m; light extinction coefficient 0.4 m^{-1})

Harvest time	Harvest Depth (m)	Live Shoot Biomass 16 August (g DW m^{-2})	Pre-harvest Shoot Biomass (g DW m^{-2})	Post-harvest Shoot Biomass (g DW m^{-2})	End-of-Year Tuber Number (N m^{-2})
Initial plant biomass 0					
None		41	n.a.	n.a.	109
15 April	1.0	41	0	0	109
———	1.5	41	0	0	109
15 June	1.0	37	5	5	121
———	1.5	6	5	1	4
15 July	1.0	37	16	15	121
———	1.5	5	16	2	4
Initial plant biomass 50 g DW m^{-2}					
None		434	n.a.	n.a.	358
15 January	1.0	431	47	43	346
———	1.5	244	47	6	503
15 April	1.0	431	93	85	346
———	1.5	242	93	12	503

From Table 6, VALLA (version 1.0), it can be concluded that a wildcelery vegetation originating from tubers alone with no other plant biomass present does not produce such a high 'nuisance' plant biomass in a tropical climate that it would hamper other uses of the water body by humans or wildlife, since peak plant biomass did not exceed 41 g DW m^{-2}. However, with 50-g initial plant biomass present, as is common in this climate (Haller 1974; Godfrey and Wooten 1997), cutting the vegetation just above the sediment surface in the period of 15 January to 15 April greatly reduces the peak biomass (from 434 to 241-244 g DW m^{-2}) but may increase the end-of-year tuber numbers. The latter increase may take place because removal of shoots greatly alleviates self-shading of the vegetation and allows more tuber classes to be finished that same year.

Whether wildcelery, in reality, produces tubers in a tropical climate or hibernates as an entire plant is still being discussed. Harvesting in January would be least expensive, since a relatively low amount of harvested biomass would have to be removed from the water body (or would decompose in situ, in case removal from the site were omitted). Such a situation would be desirable for lakes managed for use by (a) humans for recreation in summer, and (b) by tuber-grazing wildfowl in autumn.

A small drawback of the model in simulating cutting effects is that the model allows the simulated plant material that remains after harvesting to be distributed directly (i.e., during the next time-step) over the water column again, resulting in a slightly higher peak biomass, while in reality the vegetation will need more time to recover from cutting (Table 3).

Wildcelery tubers form an important food source for Canvasback ducks (*Aythya valisneria*). Foraging on these tubers continued for several weeks in November and December in the shallow (< 1-m-deep) Lake Matamuskeet, North Carolina (Lovvorn and Gillingham 1996), and in the Upper Mississippi River System, Illinois (Takekawa 1987). These birds forage randomly and by touch, over a range of 103 to 157 tubers per bout per individual, with maximally 21.6 bouts per day, resulting in a total daily consumption of 2,225 to 3,391 tubers per day. Thus, it would take a substantial wildcelery vegetation to sustain a population of 100 ducks for a month (losing 1.4 to 2.1×10^6 tubers by grazing). Although mean tuber density in Lake Matamuskeet had decreased significantly during the grazing period from 148 to 115 tubers m^{-2}, the reason for the departure of these birds to other foraging areas was not directly linked to low tuber density, but rather to decrease in viable forage habitat. Viable forage habitat for Canvasbacks is determined by the mean profit per dive, with the latter parabolically increasing with the dry weight per tuber over the range of 0.03 to 0.11g, and linearly decreasing with water depth over the range of 0.3 to 3.5 m. No foraging was done at depths >3.5 m, probably because of the relatively high cost of locomotor descent. Viable forage habitat in this case is synonymous with percentage of profitable loci, the latter being equivalent to the proportion of total habitat area that is viable foraging habitat.

The current version 1.0 of VALLA can be used as a tool to contribute to estimating the viable forage habitat for these birds by calculating the tuber size and density for wildcelery populations at various sites, with and without fluctuating water level and at various rooting depths. The tuber densities of 115 m^{-2} found after departure of the Canvasbacks to other foraging areas are higher than the typical wildcelery plant density value of 30 m^{-2}, and, thus, high enough to sustain persistence of a wildcelery vegetation over a range of 0.1- to 6-m water depth in relatively clear water. Simulations starting from tuber densities lower than 30 m^{-2}, with environmental conditions kept the same as described in VALLA (version 1.0, Table 6), indicated that initial tuber densities of 10 and 20 tubers m^{-2}, respectively, would still generate maximally 89 and 179 tubers m^{-2} in a year, allowing the wildcelery population to persist and some grazing to occur. When made spatially explicit by interfacing with a Geographic Information System (GIS), VALLA can be used as the main tool in calculating viable habitats for these birds and other animals.

5 Sensitivity Analysis

A sensitivity analysis of a simulation model is required to assess the parameters most likely to strongly affect model behavior. The current analysis was based on the effect of a change in a parameter when all other parameters are kept the same. As reference level, the nominal parameter values were chosen as presented in Table 4, under Chenango Lake, New York, conditions at a 1.4-m water depth. In a 1-year simulation beginning with a tuber size of 0.09 g DW and a tuber bank density of 233 m^{-2}, the value of the parameter under study was changed. The results were compared with those of a nominal run. Each parameter was once increased by 20 percent and once decreased by 20 percent. The relative sensitivity (RS) of a parameter was then defined as the relative change in the variable on which the effect was tested divided by the relative change in the parameter (Ng and Loomis 1984). The effects of 9 parameters on 2 variables, representing plant biomass aspects, were tested. A model variable is considered sensitive to a change in the value of a parameter at RS>0.5 and <-0.5. The current sensitivity analysis was performed over a 1-year period.

$$RS = \frac{\frac{(yield_i - yield_r)}{yield_r}}{\frac{(param_i - param_r)}{param_r}} \quad (8)$$

where

$yield_i$ = value at parameter value i

$yield_r$ = value at reference parameter value

$param_i$ and $param_r$ as above

Maximum plant biomass proved most sensitive to changes in potential CO_2 assimilation at light saturation for shoots but far less sensitive to changes in light-use efficiency. Maximum biomass was also strongly affected by changes in plant density, but less than by photosynthetic activity at light saturation. It was more strongly influenced by preanthesis than by postanthesis development rate. It was strongly influenced by individual tuber weight and relative death rate of shoots and roots. Effects of changes in relative conversion rate of tubers into plant

Table 4
Relative Sensitivity of Two Model Variables to Deviations in Parameter Values from Nominal Values as Presented in Table 3 (Results were obtained in a 1-year simulation under Chenango Lake, New York, 1978 conditions, starting from 233 tubers m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity: Maximum Live Plant Biomass	Relative Sensitivity: End-of-Year Tuber Number
Potential CO_2 assimilation rate at light saturation for shoot tips	0.0165		
	0.0200	5.00	4.46
	0.0149	3.02	2.04
Light-use efficiency	0.000011		
	0.000013	0.50	-0.73
	0.000008	0.56	1.44
Relative death rate leaves, stems, and roots	0.021		
	0.025	2.25	0.71
	0.017	-3.03	0.22
Individual tuber weight	0.090		
	0.108	3.25	-1.79
	0.072	-0.92	-0.03
Relative conversion rate of tubers into plant material	0.0576		
	0.069	2.65	-0.43
	0.046	-1.37	2.33
Relative tuber growth rate	0.247		
	0.296	1.76	-0.77
	0.198	-2.62	2.19
Plant density	30		
	36	3.39	-0.01
	24	-0.82	2.71
Preanthesis development rate	0.015		
	0.018	0.56	-2.5
	0.012	-6.04	-1.39
Postanthesis development rate	0.040		
	0.048	0.98	-2.47
	0.032	-2.19	0.24

material and of relative tuber growth rate were in the same order of magnitude and lower than those of changes in the other parameters.

In general, the same parameter changes that influenced maximum plant biomass were important determinants of end-of-year tuber numbers, with potential CO_2 assimilation at light saturation, development rates and plant density exhibiting the largest effects. This illustrates the utmost importance of the tubers for local survival and biomass production of wildcelery.

Earlier or later flowering biotypes are suited to different environments. The effect of flowering date can be tested with the model by varying the development rate of the vegetation. Slower rates represent later and faster rates represent earlier biotypes. Development rate slower or faster than the nominal rate leads to lower biomass. Faster development leads to a shorter growing season and less vegetative dry matter, incomplete light interception and lower carbohydrate availability for organ formation. At the same time, however, the rate of organ formation increases but the duration of each organ formation shortens. Intuitive prediction of biotype behavior under such highly variable climatic conditions is therefore hazardous. The model shows some promise in being able to reproduce some of these complex responses of the vegetation and may be useful in evaluating long-term implications of differences in development rate.

As far as we know, no publications exist on what the temperature requirements of aquatic plants are to traverse development from anthesis to senesced state. However, differences in postanthesis development rates for several wheat and rice cultivars are small and have little effect on yield (Van Keulen 1976).

Maximum plant biomass proved to be sensitive to changes in all development rates except an increase in preanthesis development rate, while end-of-year tuber number was sensitive to changes in all development rates except a decrease in postanthesis development rate.

6 Environmental Factor Analysis

The impacts of various changes in environmental factors were assessed using the relative sensitivity of the affected variables as "measure." For this purpose, parameter changes were based on value ranges taken from literature, which sometimes differed more than 20 percent from the nominal parameter value given in Table 3.

Climate

Climate greatly affects plant species distribution, phenological cycle, and biomass production. VALLA can be used to calculate climate change effects on the chronological timing of the phenological events and on biomass production. It can not be used to assess climate change effects on (a) plant species distribution, and (b) the phenological cycle itself, since the phenological cycle has been used for calibration (see Chapter 3). Running the model under more southern climatological conditions, i.e., changing the latitude from 42 to 27 °N, demonstrated that end-of-year tuber number is more sensitive to this climate change than maximum plant biomass (Table 5).

Light Reflection Coefficient by Water Surface

The irradiance reflected by the water surface usually averages about 6 percent over a day. The values of this parameter tested were 0 and 1. Reflection may theoretically have the value 0 when no reflection occurs at a 90° incoming angle of the radiation on a completely calm water surface (wind and wave action are minimal). The highest value of 1 may occur at a near to 180° incoming angle of the radiation and at very rough water surfaces.

Increasing the light reflection coefficient to 1 annihilated plant biomass within the year. That nevertheless low RS values were found (Table 5) is an artifact of the calculation method employed. Decreasing the light reflection coefficient increased maximum biomass and end-of-year tubers to a relatively small extent, probably because the majority of the plant material is located in the lower half of the water column (Table 5).

Table 5
Environmental Factor Analysis, Expressed as Relative Sensitivity of Two Model Variables to Deviations in Parameter Values from Nominal Values as Presented in Table 3 (Results were obtained in a 1-year simulation under Chenango Lake, New York, 1978 conditions, starting from 233 tubers m^{-2})

Parameter Name	Parameter Value	Relative Sensitivity: Maximum Live Plant Biomass	Relative Sensitivity: End-of-Year Tuber Number
Climate			
Chenango Lake (1978)	Latitude 42° N	-	-
Ft. Lauderdale ponds (1975-84)	Latitude 27° N	-0.49	-0.87
Light reflection coefficient by water surface	0.06		
	1.00 (+1,567%)	-0.06	-0.06
	0.00* (-100%)	-0.43	-0.05
Light extinction coefficient water column	0.43		
	0.52 (+20%)	2.09	0.04
	0.34 (-20%)	-2.79	0.66
Water depth	1.4		
	1.7 (+20%)	1.47	-2.16
	1.1 (-20%)	-2.43	0.48

Note: To enable calculation of the RS, a very low value of 0.000001 was used.

Light Extinction Coefficient of Water Column

A light extinction coefficient averaging 0.43 m^{-1} is used for nominal runs of the model (Chenango Lake, New York).

Changing the light extinction coefficient of the water column demonstrated large effects on maximum plant and smaller ones on end-of-year tuber numbers. A nominal value of 2 m^{-1} has been found typical for eutrophic fen lakes where submersed vegetation just can survive (Best, De Vries, and Reins 1985).

Water Depth

VALLA has been calibrated for a water depth of 1.4 m, the rooting depth of an extensively studied wildcelery community in Chenango Lake, New York. The model has the capability to respond to fluctuations in water level between years and within year, by distributing or redistributing plant biomass over the desired water depth (number of water layers; see Chapter 3). This technique for biomass distribution over the vertical axis of the community works well and gives realistic outcomes over a depth range of 0.2 to 6 m.

Running VALLA at an increased or decreased water depth showed considerable effects on maximum plant biomass and end-of-year tuber number (Table 5).

The RS of peak plant biomass and of end-of-year tuber number to changes in water depth was in the same order of magnitude as to changes in light extinction coefficient.

The current sensitivity and environmental analyses give indications of the sensitivity of maximum plant biomass and end-of-year tuber number for variations in plant parameters and environmental factors over a 1-year period. It is to be expected, however, that the small changes that occurred over this relatively short period will increase with time and that extrapolations in time will yield information on the likelihood for plant populations to ultimately persist or become extinct. Particularly, increased water turbidity, because of increased phytoplankton or periphyton growth stimulated by eutrophication, increased erosion/resuspension, and seasonal herbivory have been mentioned as decisive for the persistence of submersed plant populations.

7 Application Possibilities

VALLA can be used to assess behavior of a wildcelery community under various site-specific and climatological conditions as demonstrated in Chapters 4, 5, and 6, and the simulation model can be run with user-specified input values for plant biomass, tuber size/tuber number concurrently initiated, and tuber bank density.

Effects of man-made activities, like mechanical harvesting at different times and at various water depths, and like water level and water quality management can also be calculated using the model. Thus, in the latter case it can be used as a tool for aquatic plant and water management agencies (see for instance Bartell et al. 2000).

The current version of VALLA has been developed as a stand-alone simulation model. It can be relatively easily modified to communicate with ecosystem models because it is written in FORTRAN77 and its structure is simple. It is planned to link VALLA to a GIS through an appropriate interface like AEGIS+ (Luyten et al. 1994). To facilitate use of the current model, a user manual has been prepared (Best and Boyd 2001a).

8 Discussion

The current model gives a reasonable description of the dynamics in plant biomass and tuber numbers of an established wildcelery population under a variety of field conditions. As can be expected, the model is very sensitive to environmental changes affecting the light climate and, consequently, the carbon flow through the plant.

Extinction of light by periphyton has not been included in VALLA because no field data on periphyton biomass concomitant with photosynthetic activity are available at this time. Light attenuation by periphyton is expected to have large effects on submersed macrophytes with biomass usually remaining below the water surface (like *Vallisneria americana*; Titus and Adams 1979a), and those with most of their biomass concentrated just above the hydrosoil (like *Ceratophyllum demersum* (Best and Dassen 1987; Best and Jacobs 1990).

Senescence, resulting in decreasing photosynthetic activity in aging plant parts, has been included into the model formulation, but because of lack of data, this feature has not been activated. However, effects of senescence over the vertical plant axis proved to be negligible in other submersed plant species (Eurasian watermilfoil; Best and Boyd 1999a).

References

Amthor, J. S. (1984). "The role of maintenance respiration in plant growth," *Plant, Cell, and Environment* 7, 561-569.

Barko, J. W., and Filbin, G. J. (1982). "Influences of light and temperature on chlorophyll composition in submersed freshwater macrophytes," *Aquatic Botany* 15, 249-255.

Barko, J. W., Hardin, D. G., Matthews, M. S. (1984). "Interactive influences of light and temperature on the growth and morphology of submersed freshwater macrophytes." Technical Report A-84-3, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Bartell, S. M., Campbell, K. R., Best, E. P. H., and Boyd, W. A. (2000). "Interim report for the Upper Mississippi River System-Illinois Waterway System Navigation Study: Ecological risk assessment of the effects of the incremental increase of commercial navigation traffic (25, 50, 75, and 100% increase of 1992 baseline traffic) on submersed aquatic plants in the main channel borders," ENV Report 17, U.S. Army Engineer Districts, Rock Island, St. Louis, and St. Paul.

Bellrose, F. C., Havera, S. P., Paveglio, F. L., and Steffeck, D. W. (1983). "Fate of the lakes in the Illinois River valley." *Illinois Natural History Survey Biology Note* 119.

Best, E. P. H. (1981). "A preliminary model for growth of *Ceratophyllum demersum* L.," *Verhaendlungen des Internationales Vereinigung fuer Limnologie* 21, 1484-1491.

_____. (1982). "Hormonal interactions in *Ceratophyllum demersum*," *Aquatic Botany* 13, 87-95.

Best, E. P. H., and Boyd, W. A. (1996). "A simulation model for growth of the submersed aquatic macrophyte hydrilla (*Hydrilla verticillata* (L.F.) Royle," Technical Report A-96-8, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Best, E. P. H., and Boyd, W. A. (1999a). "A simulation model for growth of the submersed aquatic macrophyte Eurasian watermilfoil (*Myriophyllum spicatum* L)," Technical Report E-99-3, U.S. Army Engineer Research and Development Center, Vicksburg, MS.

_____. (1999b). "MILFO (version 1.0): A simulation model for growth of Eurasian watermilfoil—User's guide," Instruction Report A-99-1, U.S. Army Engineer Research and Development Center, Vicksburg, MS.

_____. (2001a) "VALLA (Version 1.0): A simulation model for growth of American wildcelery," ERDC/EL TR-01-_ (in preparation), U.S. Army Engineer Research and Development Center, Vicksburg, MS.

_____.(2001b) "A simulation model for growth of the submersed aquatic macrophyte sago pondweed (*Potamogeton pectinatus* L.)," ERDC/EL TR-01-_ (in preparation), U.S. Army Engineer Research and Development Center, Vicksburg, MS.

Best, E. P. H., and Dassen, J. H. A. (1987). "Biomass, stand area, primary production characteristics and oxygen regime of the *Ceratophyllum demersum* L. population in Lake Vechten, The Netherlands," *Archiv fuer Hydrobiologie/Supplement* 76, 347-367.

Best, E. P. H., De Vries, D., and Reins, A. (1985). "The macrophytes in the Loosdrecht Lakes: A story of their decline in the course of eutrophication," *Verhaendlungen des Internationalen Vereinigungs Theoretische und Angewandte Limnologie* 22, 868-875.

Best, E. P. H., and Jacobs, F. H. H. (1990). "Potential and actual production of submerged aquatic angiosperms common in temperate regions." *Proceedings, 8th Symposium on Aquatic Weeds*, 39-47.

Blanch, S. J., Ganf, G. G., Walker, K. F. (1998). "Growth and recruitment in *Vallisneria americana* as related to average irradiance in the water column," *Aquatic Botany* 61, 181-205.

Bowes, G., Holaday, A. C., Haller, W. T. (1979). "Seasonal variation in the biomass, tuber density and photosynthetic metabolism in three Florida lakes," *Journal of Aquatic Plant Management* 17, 61-65.

Boyd, W. A., and Best, E. P. H. (1996). "HYDRIL (Version 1.0): A simulation model for growth of Hydrilla," Instruction Report A-96-1, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Britton, N. L., and Brown, A. (1913). "An illustrated flora of the northern United States, Canada, and the British Possessions," Vol 1, 2nd Ed. Charles Scribner's Sons, New York, 680 pp.

Catling, P. M., Spicer, K. W., Biernacki, M., Doust, J. L. (1994). "The biology of Canadian weeds. 103. *Vallisneria americana* Michx.," *Canadian Journal of Plant Science* 74, 883-897.

Chapman, A. W. (1883). "Flora of the southern United States," 2nd ed., Iveson, Blakeman, Taylor, New York, 698 pp.

Choudhuri, G. N. (1966). "Seed germination and flowering in *Vallisneria spiralis*," *Northwest Science* 40, 31-35.

Collins, C. D., and Wlosinski, J. H. (1985). "A macrophyte submodel for aquatic ecosystems," *Aquatic Botany* 33, 191-206.

Correll, D. S., and Correll, H. B. (1972). "Aquatic and wetland plants of the Southwestern United States," Stanford University Press, Stanford, CA, Vol I, 856 pp.

Donnermeyer, G. N. (1982). "The quantity and nutritive quality of *Vallisneria americana* biomass, in Navigation Pool No. 9 of the Upper Mississippi River," M.S. Thesis, University of Wisconsin, La Crosse, WI.

Donnermeyer, G. N., and Smart, M. M. (1985). "The biomass and nutritive potential of *Vallisneria americana* Michx. in Navigation Pool 9 of the Upper Mississippi River," *Aquatic Botany* 22, 33-44.

Fernald, M. L. (1918). "The diagnostic character of *Vallisneria americana*," *Rhodora* 20, 108-110.

Fernald, M. L. (1950). *Gray's manual of botany*. American Book Company, New York, NY, 8th ed., 1632 pp.

Giesen, W. B. J. T., Van Katwijk, M. M., and Den Hartog, C. (1990). "Eelgrass condition and turbidity in the Dutch Wadden Sea," *Aquatic Botany* 37, 71-85.

Gijzen, H. (1985). "Simulatie van drogestof-produktie en de Leaf Area Index van cassave," *M.S. Thesis, Department of Tropical Crop Science, Wageningen Agricultural University*, The Netherlands (In Dutch).

Gleason, H. A. (1968). *The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada*. Hafner, New York, NY, vol 1, 482 pp.

Godfrey, R. K., and Wooten, J. W. (1997). *Aquatic and wetland plants of Southeastern United States, monocotyledons*. The University of Georgia Press, Athens, 711 pp.

Golterman, H.L. (1975). *Physiological limnology. An approach to the physiology of lake ecosystems*. Elsevier Scientific Publishing Company, Amsterdam, 489 pp.

Goudriaan, J. (1986). "A simple and fast numerical method for the computation of daily totals of crop photosynthesis," *Agricultural and Forest Meteorology* 38, 251-255.

Goudriaan, J., Van Keulen, H., and Van Laar, H. H. (1992). "Crop growth model for potential production (SUCROS1)," *Simulation of crop growth for potential and water-limited production situations (as applied to spring wheat).* Postgraduate course 'Simulation of plant growth and crop production.' Pontignano, Siena, Italy, 3-12 November, 1992, 1-25.

Gray, A. (1848). *A manual of the botany of the northern United States*. 1st ed. Metcalf, Cambridge, 710 pp.

Gray, A. (1874). *A manual of the botany of the northern United States*. 5th ed. Iveson, Blakeman, Taylor, New York, 703 pp.

Griffin, K. L. (1994). "Caloric estimates of construction cost and their use in ecological studies," *Functional Ecology* 8, 551-562.

Haller, W. T. (1974). "Photosynthetic characteristics of the submersed aquatic plants Hydrilla, southern naiad, and Vallisneria," Ph.D. diss., University of Florida, Gainesville, FL, 88 pp.

Hootsmans, M. J. M. (1991). "A growth analysis model for *Potamogeton pectinatus* L." *Macrophytes, a key to understanding changes caused by eutrophication in shallow freshwater ecosystems*. M. J. M. Hootsmans and J. E. Vermaat, ed., *IHE Report Series* 21, Delft, The Netherlands, 263-311.

Hunt, R. (1982). *Plant growth curves*. Arnold, London.

Ikusima, I. (1970). "Ecological studies on the productivity of aquatic plant communities. IV. Light condition and community photosynthetic production," *Botanical Magazine of Tokyo* 83, 330-340.

Kausik, S. B. (1939). "Pollination and its influence on the behavior of the pistillate flower in *Vallisneria spiralis*," *American Journal of Botany* 26, 207-211.

Kimber, A., Korschgen, C. E., and Van der Valk, A. G. (1995). "The distribution of *Vallisneria americana* seeds and seedling light requirements in the Upper Mississippi River," *Canadian Journal of Botany* 73, 1966-1973.

Klaine, S. J., and Ward, C. H. (1984). "Environmental and chemical control of vegetative dormant bud production in *Hydrilla verticillata*," *Annals of Botany* 53, 503-514.

Kooman, P. L. (1995). "Genotype-environment interaction in potato 2: Dry matter allocation and duration of the growth cycle, *Yielding ability of potato crops as influenced by temperature and daylength*," Ph.D. thesis, Agricultural University, Wageningen, Chapter 5; 71-89.

Korschgen, C. E., and Green, W. L. (1988). "American wild celery (*Vallisneria americana*): Ecological considerations for restoration," Fish and Wildlife Technical Report 19, U. S. Department of the Interior, Fish and Wildlife Service, Washington DC, 24 pp.

Korschgen, C. E, Green, W. L., and Kenow, K. P. (1997). "Effects of irradiance on growth and winter bud production by *Vallisneria americana* and consequences to its abundance and distribution," *Aquatic Botany* 58, 1-9.

Lokker, C., Susko, D., Lovett-Doust, L., and Lovett-Doust, J. (1994). "Population genetic structure of *Vallisneria americana*, a dioecious clonal macrophyte," *American Journal of Botany* 81, 1004-1012.

Long, R. W., and Lakela, O. (1971). *A flora of tropical Florida, a manual of the seed plants and ferns of southern peninsular Florida.* University of Miami Press, Coral Gables, FL, 962 pp.

Lovvorn, J. R. (1989). "Distributional responses of canvasback ducks to weather and habitat change," *Journal of Applied Ecology* 26, 113-130.

Lovvorn, J. R., and Gillingham, M. P. (1996). "Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores," *Ecology* 77, 435-451.

Lowden, R. M. (1982). "An approach to the taxonomy of *Vallisneria* L. (Hydrocharitaceae)." *Aquatic Botany* 13, 269-298.

Luyten, J. C., Jones, J. W., Calixte, J. P., Hoogenboom, G., and Negahban, B. (1994). "AEGIS+. Agricultural and Environmental Geographic Information System plus. Version 2.0." *User's and Developer's Manual. Research Report AGE* No.94-1, Agricultural Engineering Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL.

Marie-Victorin, Frere. (1943). "Les Vallisneries Americaines," *Contributions de l' Institut Botanique de l'Universite de Montreal* 46, 1-38.

McFarland, D. G., and Rogers, S. R. (1998). "The aquatic macrophyte seed bank in Lake Onalaska, Wisconsin," *Journal of Aquatic Plant Management* 36, 33-39.

Ng, E., and Loomis, R.S. (1984). "Simulation of growth and yield of the potato crop." *Simulation Monographs*, Pudoc, Wageningen, 147 pp.

Nichols, S. A. (1999). "Distribution and habitat descriptions of Wisconsin lake plants," *Wisconsin Geological and Natural History Survey Bulletin* 96, 229.

Penning de Vries, F. W. T. (1975). "The cost of maintenance processes in plant cells," *Annals of Botany* 39, 77-92.

Penning de Vries, F. W. T., Jansen, D. M., Ten Berge, H. F. M., and Bakema, A. (1989a). "Morphological development and assimilate partitioning." *Simulation of ecophysiological processes of growth in several annual crops. Chapter 3*, Pudoc, Wageningen, 49-56.

Penning de Vries, F. W. T., Jansen, D. M., Ten Berge, H. F. M., and Bakema, A. (1989b). "Morphological development and assimilate partitioning." *Simulation of ecophysiological processes of growth in several annual crops. Chapter 3*, Pudoc, Wageningen, 73-115.

Penning de Vries, F. W. T., and Van Laar, H. H. (1982a). "Simulation of growth processes and the model BACROS." *Simulation of plant growth and crop production*. Pudoc, Wageningen, 99-102.

_____. (1982b). "Simulation of growth processes and the model BACROS." *Simulation of plant growth and crop production*, Pudoc, Wageningen, 114-131.

Rabbinge, R., and De Wit, C. T. (1989). "Theory of modelling and systems management." *Simulation and systems management in crop protection.* R. Rabbinge, S. A. Ward, and H. H. van Laar, ed., *Chapter 1*. Simulation Monographs 32, Pudoc, Wageningen, 1-12.

Rogers, S. J. (1994). "Preliminary evaluation of submersed macrophyte changes in the Upper Mississippi River," *Lake and Reservoir Management* 10, 35-38.

Scheffer, M. (1991). "On the prediction of aquatic vegetation in shallow lakes." *Memorie dell' Istituto Italiano di Idrobiologia* 48, 207-217.

Scheffer, M., Bakema, A. H., and Wortelboer, F. G. (1993). "MEGAPLANT: A simulation model of the dynamics of submerged plants," *Aquatic Botany* 45, 341-356.

Sculthorpe, C. D. (1967). *The biology of aquatic vascular plants*. Edward Arnold (Publishers) Ltd., London, 307.

Spencer, D. F., Ksander, G. G., and Whitehand, L. C. (1994). "Estimating the abundance of subterranean propagules of submersed aquatic plants," *Freshwater Biology* 31, 191-200.

Spencer, D. F., Ryan, F. J., and Ksander, G. G. (1997). "Construction costs for some aquatic plants," *Aquatic Botany* 56, 203-214.

Spink, A., and Rogers, S. (1996). "The effects of a record flood on the aquatic vegetation of the Upper Mississippi River System: Some preliminary findings." *Hydrobiologia* 340, 51-57.

Spitters, C.J.T. (1986). "Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. II. Calculation of canopy photosynthesis," *Agricultural and Forest meteorology* 38, 231-242.

Svedelius, N. (1932). "On the different types of pollination in *Vallisneria spiralis* L. and *Vallisneria americana* Michx.," Svenska Botanische Tidskrift 26, 1-12.

Takekawa, J. Y. (1987). "Energetics of canvasbacks staging on an Upper Mississippi River pool during fall migration," Ph.D. diss., Iowa State University, Ames, IA.

Thornley, J.H.M., and Johnson, I.R. (1990a). "Temperature effects on plant and crop processes." *Plant and crop modelling. A mathematical approach to plant and crop physiology*. Clarendon Press, Oxford, 139-144.

Thornley, J.H.M., and Johnson, I.R. (1990b). "Plant growth functions." *Plant and crop modelling. A mathematical approach to plant and crop physiology.*" Clarendon Press, Oxford, 74-89.

Titus, J. E. (1977). The comparative physiological ecology of three submersed macrophytes." Ph.D. Thesis, University of Wisconsin, Madison, WI.

Titus, J., and Adams, M. A. (1979a). "Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllym spicatum* L. and *Vallisneria americana* Michx.,"*Oecologia* 40, 273-286.

Titus, J. E., and Adams, M. A. (1979b). "Comparative storage utilization patterns in the submersed macrophytes, *Myriophyllum spicatum* and *Vallisneria americana,*" *The American Midland Naturalist* 102, 263-272.

Titus, J. E., Feldman, R. S., and Grise, D. (1990). "Submersed macrophyte growth at low pH. I. CO_2 enrichment effects with fertile sediment," *Oecologia* 84, 307-313.

Titus, J., Goldstein, R. A., Adams, M. A., Mankin, J. B., O'Neill, R. V., Weiler, P. R., Shugart, H. H., and Booth, R. S. (1975). "A production model for *Myriophyllum spicatum* L.," *Ecology* 56, 1129-1138.

Titus, J. E., and Hoover, D. T. (1991). "Toward predicting reproductive success in submersed freshwater angiosperms," *Aquatic Botany* 41, 111-136.

Titus, J. E., and Stephens, M. D. (1983). "Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake," *Oecologia* 56, 23-29.

Titus, J. E., and Stone, W. H. (1982). "Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH," *Limnology and Oceanography* 27, 151-160.

Van, T. K., Haller, W. T., and Bowes, G. (1976). "Comparison of the photosynthetic characteristics of three submersed aquatic plants," *Plant Physiology* 58, 761-768.

_____. (1978). "Some aspects of the competitive biology of Hydrilla." *Proceedings, 5th EWRS International Symposium on Aquatic Weeds. Amsterdam (The Netherlands)*, 117-126.

Van Keulen, H. (1976). "Evaluation of models." *Critical evaluation of systems analysis in ecosystems research and management.* G. W. Arnold and C. T. de Wit, ed., Simulation Monographs, Pudoc, Wageningen, 22-29.

Van Kraalingen, D. W. G. (1995). "The FSE system for crop simulation." *AB-DLO Report.* Wageningen, The Netherlands, 53 pp.

Wetzel, R. L., and Neckles, H. A. (1996). "A model of *Zostera marina* L. photosynthesis and growth: Simulated effects of selected physical-chemical variables and biological interactions," *Aquatic Botany* 26, 307-323.

Williams, K., Percival, F., Merino, J., and Mooney, H.A. (1987). "Estimation of tissue construction cost from heat combustion and organic nitrogen content," *Plant Cell and Environment* 10, 725-734.

Appendix A
Model Listing

```
* ------------------------------------------------------------------------------ *
* SUBROUTINE MODEL                                                               *
* Authors: Elly Best & Will Boyd                                                 *
* Date   : 18 August 1999                                                        *
* Purpose: This subroutine is the translated FST file                            *
*                                                                                *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                *
* name      type    meaning                                  units      class*
* -----     -----   ---------                                -----      -----*
* DELT      R4      Time step of integration                 d          I    *
* DOY       R4      Day number within year of simulation (REAL) d       I    *
* FILEIN    C*      Name of file with input model data       -          I    *
* FINTIM    R4      Finish time of simulation (=day number)  d          I    *
* IDOY      I4      Day number within year of simulation (INTEGER) d    I    *
* ITASK     I4      Task that subroutine should perform      -          I    *
* IUNITD    I4      Unit of input file with model data       -          I    *
* IUNITO    I4      Unit of output file                      -          I    *
* IUNITL    I4      Unit number for log file messages        -          I    *
* IYEAR     I4      Year of simulation (INTEGER)             y          I    *
* LAT       R4      Latitude of site                         dec.degr.  I    *
* LONG      R4      Longitude of site                        dec.degr.  I    *
* ELEV      R4      Elevation of site                        m          I    *
* OUTPUT    L4      Flag to indicate if output should be done -         I    *
* RAIN      R4      Daily amount of rainfall                 mm.d-1     I    *
* RDD       R4      Daily shortwave radiation                J.m-2.d-1  I    *
* STTIME    R4      Start time of simulation (=day number)   d          I    *
* TERMNL    L4      Flag to indicate if simulation is to stop -         I/O  *
* TMMN      R4      Daily minimum temperature                degrees C  I    *
* TMMX      R4      Daily maximum temperature                degrees C  I    *
* VP        R4      Early morning vapor pressure             kPa        I    *
* WN        R4      Daily average wind speed                 m/s        I    *
* WSTAT     C6      Status code from weather system          -          I    *
* WTRTER    L4      Flag whether weather can be used by model -         O    *
* YEAR      R4      Year of simulation (REAL)                y          I    *
*                                                                                *
* Fatal error checks: if one of the characters of WSTAT = '4', indicates missing weather *
* Warnings       : none                                                          *
* Subprograms called: models as specified by the user                            *
* File usage     : IUNITD,IUNITD+1,IUNITO,IUNITO+1,IUNITL                        *
* ------------------------------------------------------------------------------ *

      SUBROUTINE MODEL (ITASK , IUNITD, IUNITO, IUNITL,
     &                  FILEIN,
     &                  OUTPUT, TERMNL,
     &                  DOY   , IDOY  , YEAR  , IYEAR,
     &                  TIME  , STTIME, FINTIM, DELT ,
     &                  LAT   , LONG  , ELEV  , WSTAT , WTRTER,
     &                  RDD   , TMMN  , TMMX  , VP    , WN, RAIN)

*----Title of the program
*     <Fill in your title here>
*     Valla1
```

```
      IMPLICIT REAL (A-Z)

*-----Formal parameters

      INTEGER  ITASK , IUNITD, IUNITO, IUNITL, IDOY, IYEAR
      LOGICAL  OUTPUT, TERMNL, WTRTER
      CHARACTER*(*) FILEIN, WSTAT
      REAL DOY, YEAR, TIME, STTIME, FINTIM, DELT
      REAL LAT, RDD, TMMN, TMMX, VP, WN, RAIN
      REAL TMAX(365), TMIN(365)

*-----Standard local declarations
      INTEGER IWVAR,ITOLD,IDAY,DDELAY,SSURPR
      CHARACTER WUSED*6

*-----State variables, initial values and rates
      REAL DVS   , NUL   , DVR
      REAL TREMOB, IREMOB,TMPSUM
      REAL TWLVD , IWLVD , DLV
      REAL TWLVG , IWLVG , NGLV
      REAL TWSTD , IWSTD , DST
      REAL TWSTG , IWSTG , NGST
      REAL TWRTD , IWRTD , DRT
      REAL TWRTG , IWRTG , NGRT
      REAL TMP2  , INTUB

*-----Model parameters
      REAL AMX   , CVT   , DAYEM , DELAY ,REDAM
      REAL NPL   , CRIFAC, SURPER, TWTUB ,TWTUBD
      REAL RC    , TBASE
      REAL ROC   , TL    , RCSHST, EE    , RDTU
      REAL NNTUB , NGTUB , NTUBD , NDTUB , RTR
      REAL TWGTUB, TWNTUB, NTUBPD, NINTUB, TWCTUB
      REAL HAR   , HARDAY, HARDEP

*-----Auxiliary variables
      REAL AMAX    , AMTMP , ASRQ    , COSLD  , WTMP
      REAL DAVTMP, DAY      , DAYL    , YRNUM , WST
      REAL DDTMP  , DS0      , DSINB   , DSINBE
      REAL DTEFF   , DTGA    , FGROS  , FLV     , FRT
      REAL FST      , GLV     , GPHOT  , GRT    , GST
      REAL GTW     , MAINT   , MAINTS, NTM    , PI
      REAL RDR     , RDS     , REMOB , SC      , SUM
      REAL TGWM   , SINLD    , TGW    , TEFF    , TRANS
      REAL TW      , WLV     , WRT    , SURFAC

*-----AFGEN functions
*     REAL AMDVST
*     INTEGER IMAMDV, ILAMDV
*     PARAMETER (IMAMDV =  40)
*     DIMENSION AMDVST(IMAMDV)
      REAL AMTMPT
      INTEGER IMAMTM, ILAMTM
      PARAMETER (IMAMTM =  40)
      DIMENSION AMTMPT(IMAMTM)
      REAL DPTT
```

```
      INTEGER IMDPT, ILDPT
      PARAMETER (IMDPT =  730)
      DIMENSION DPTT (IMDPT)
      REAL FLT
      INTEGER IMFLT, ILFLT
      PARAMETER (IMFLT  =  40)
      DIMENSION FLT (IMFLT)
      REAL FLVT
      INTEGER IMFLVT, ILFLVT
      PARAMETER (IMFLVT =  40)
      DIMENSION FLVT (IMFLVT)
      REAL FRTT
      INTEGER IMFRTT, ILFRTT
      PARAMETER (IMFRTT =  40)
      DIMENSION FRTT (IMFRTT)
      REAL FSTT
      INTEGER IMFSTT, ILFSTT
      PARAMETER (IMFSTT =  40)
      DIMENSION FSTT (IMFSTT)
      REAL LT, KT
      INTEGER IMN1,ILT,IKT
      PARAMETER (IMN1   =  730)
      DIMENSION LT(IMN1), KT(IMN1)
      REAL NTMT, TGWMT
      INTEGER IMMEAS, ILMEAS
      PARAMETER (IMMEAS =  40)
      DIMENSION NTMT(IMMEAS), TGWMT(IMMEAS)
      REAL RDRT
      INTEGER IMRDRT, ILRDRT
      PARAMETER (IMRDRT =  40)
      DIMENSION RDRT  (IMRDRT)
      REAL RDST
      INTEGER IMRDST, ILRDST
      PARAMETER (IMRDST =  40)
      DIMENSION RDST  (IMRDST)
      REAL TEFFT
      INTEGER IMTEFF, ILTEFF
      PARAMETER (IMTEFF =  40)
      DIMENSION TEFFT(IMTEFF)
      REAL WTMPT
      INTEGER IMWTMP, ILWTMP
      PARAMETER (IMWTMP =  730)
      DIMENSION WTMPT (IMWTMP)

*----Used functions
      REAL LINT  , INSW
      SAVE

      DATA ITOLD /4/
*----Code for the use of RDD, TMMN, TMMX, VP, WN, RAIN  (in that order)
*     A letter 'U' indicates that the variable is used in calculations
      DATA WUSED/'UUU---'/
```

```
*----Check weather data availability
      IF (ITASK.EQ.1.OR.ITASK.EQ.2.OR.ITASK.EQ.4) THEN
         DO 10 IWVAR=1,6
*-----Is there an error in the IWVAR-th weather variable ?
            IF (WUSED(IWVAR:IWVAR).EQ.'U' .AND.
     &          WSTAT(IWVAR:IWVAR).EQ.'4') THEN
                WTRTER = .TRUE.
                TERMNL = .TRUE.
                ITOLD  = ITASK
                RETURN
            END IF
10       CONTINUE
      END IF

      IF (ITASK.EQ.1) THEN
*                                                        *
*              INITIALIZATION  SECTION                   *
*            ============================                *
*----Send title to output file                           *

*----Open input file
            CALL RDINIT (IUNITD, IUNITL, FILEIN)

*----Read 1st value in MODEL.DAT file ... year number
            CALL RDSREA ('YRNUM ',YRNUM )

*----Read initial states
            CALL RDSREA ('INTUB  ',INTUB )
            CALL RDSREA ('IREMOB',IREMOB)
            CALL RDSREA ('IWLVD ',IWLVD )
            CALL RDSREA ('IWLVG ',IWLVG )
            CALL RDSREA ('IWRTD ',IWRTD )
            CALL RDSREA ('IWRTG ',IWRTG )
            CALL RDSREA ('IWSTD ',IWSTD )
            CALL RDSREA ('IWSTG ',IWSTG )
            CALL RDSREA ('NUL   ',NUL   )
            CALL RDSREA ('REMOB ',REMOB )

*----Read model parameters
            CALL RDSREA ('AMX     ',AMX   )
            CALL RDSREA ('CRIFAC  ',CRIFAC)
            CALL RDSREA ('CVT     ',CVT   )
            CALL RDSREA ('DAYEM   ',DAYEM )
            CALL RDSREA ('DELAY   ',DELAY )
            CALL RDSREA ('EE      ',EE    )
            CALL RDSREA ('HAR     ',HAR   )
            CALL RDSREA ('HARDAY ',HARDAY)
            CALL RDSREA ('HARDEP ',HARDEP)
            CALL RDSREA ('NDTUB  ',NDTUB )
            CALL RDSREA ('NINTUB  ',NINTUB)
            CALL RDSREA ('NPL     ',NPL   )
            CALL RDSREA ('RC      ',RC    )
            CALL RDSREA ('RCSHST ',RCSHST)
```

```
      CALL RDSREA ('RDTU    ',RDTU  )
      CALL RDSREA ('REDAM  ',REDAM )
      CALL RDSREA ('ROC     ',ROC   )
      CALL RDSREA ('RTR     ',RTR   )
      CALL RDSREA ('SURPER ',SURPER)
      CALL RDSREA ('TBASE   ',TBASE )
      CALL RDSREA ('TL      ',TL    )
      CALL RDSREA ('TWCTUB',TWCTUB)

*----Read AFGEN functions
      CALL RDAREA ('AMTMPT',AMTMPT,IMAMTM,ILAMTM)
      CALL RDAREA ('DPTT    ',DPTT  ,IMDPT ,ILDPT)
      CALL RDAREA ('FLT     ',FLT   ,IMFLT , ILFLT)
      CALL RDAREA ('FLVT    ',FLVT  ,IMFLVT,ILFLVT)
      CALL RDAREA ('FSTT    ',FSTT  ,IMFSTT,ILFSTT)
      CALL RDAREA ('FRTT    ',FRTT  ,IMFRTT,ILFRTT)
      CALL RDAREA ('KT      ',KT    ,IMN1  ,IKT   )
      CALL RDAREA ('LT      ',LT    ,IMN1  ,ILT   )
      CALL RDAREA ('NTMT    ',NTMT  ,IMMEAS,ILMEAS)
      CALL RDAREA ('RDRT    ',RDRT  ,IMRDRT,ILRDRT)
      CALL RDAREA ('RDST    ',RDST  ,IMRDST,ILRDST)
      CALL RDAREA ('TEFFT   ',TEFFT ,IMTEFF,ILTEFF)
      CALL RDAREA ('TGWMT',TGWMT ,IMMEAS,ILMEAS)
      CALL RDAREA ('WTMPT',WTMPT ,IMWTMP,ILWTMP)

***           INITIAL CALCULATIONS              ***
*             ======================              *

*----Initially known variables to output
*     Send title(s) to OUTCOM

*----Initialize state variables
*     Start at the beginning of the developmental cycle
        DVS   = NUL
        TMPSUM = NUL

*----Initialize counter KCOUNT & SURFACE
     KCOUNT = 0
     SURFAC = 0

*----DELAY and SSURPR variables are set from a REAL to an INTEGER
     DDELAY = DELAY
     SSURPR = SURPER

*----Initialize weights of plant organs
        IF (YRNUM .EQ. 1.)THEN
        TWLVD  = IWLVD
        TWLVG  = IWLVG
        TWSTD  = IWSTD
        TWSTG  = IWSTG
        TWRTD  = IWRTD
        TWRTG  = IWRTG
        ENDIF
```

```
*----Initialize remobilization
          TREMOB = IREMOB

*----Initialize tuber numbers and weight
          NNTUB  = 0.0
        IF (NDTUB .LT. 30.)NPL = NDTUB
          NGTUB  = NPL
        IF(YRNUM.EQ.1.)NTUBD  = RDTU * NDTUB * TEFF
        NDTUB  = NDTUB - (NTUBD-NTUBPD)
          TWGTUB  = NPL * INTUB
          TWNTUB  = 0.0

      ELSE IF (ITASK.EQ.2) THEN

***             RATES OF CHANGE             ***
*             ====================            *

*----Weights of plant organs
          WLV  =  TWLVG  + TWLVD
          WST  =  TWSTG  + TWSTD
          WRT  =  TWRTG  + TWRTD
          TGW  =  TWLVG  + TWSTG + TWRTG

*----Total live weight never >496 g DW/m2; cf. Haller 1974.
          TGW   = AMIN1 (TGW, 496.)

****              RATE CALCULATIONS              ***
*             ==========================          *

*----Julian day number
          DAY = 1.+MOD (TIME-1.,365.)

*----If water temperatures are available, temperature dependent processes are related to
*         water temperature; otherwise they are related to air temperature with a lag period in
*         day(s) to be chosen by substituting number given for DELAY in MODEL.DAT

          WTMP = LINT (WTMPT,ILWTMP,DAY)
          DPT  = LINT (DPTT,ILDPT,DAY)
          IDAY = DAY

          TMAX(IDAY) = TMMX
          TMIN(IDAY) = TMMN
      IF (DAY .LE. 7.0) THEN
          DAVTMP = 0.5 * (TMAX(1)+TMIN(1))
        DDTMP  = AMAX1(TMAX(1) - 0.25 * (TMAX(1)-TMIN(1)),5.)
      ELSE
        DAVTMP = 0.5 * (TMAX(IDAY-DDELAY)+TMIN(IDAY-DDELAY))
        DDTMP  = AMAX1(TMAX(IDAY-DDELAY) - 0.25 *
     &          (TMAX(IDAY-DDELAY)-TMIN(IDAY-DDELAY)),5.)
      ENDIF

      IF (DAVTMP .LT. 5.0)DAVTMP = 5.0
```

```
        IF (WTMP .GT. 0.0) THEN
        DAVTMP = WTMP
        DDTMP  = WTMP
        ENDIF

*----Effective temperature influencing remobilization and translocation processes

     TEFF = LINT(TEFFT,ILTEFF,DDTMP)

*----Relative tuber growth rate
        RTRL   = RTR * TEFF

*----Measured tuber numbers and measured total live plant dry weight
        NTM  = LINT (NTMT,ILMEAS,DAY)
        TGWM = LINT (TGWMT,ILMEAS,DAY)

*----SBRT ASTRO call to introduce day length into MAIN
    CALL ASTRO
   $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Tuber behavior. Sprouting of tubers leads to carbohydrate remobilization to form
*       new plants, is related to DVS (calibrated to proper day length and temperature)
*       provided tubers are present; sprouting can only take place before normal anthesis
*       time (DVS=1). If plants lose their biomass after DVS = 1, no new tubers
*       sprout that same year. Tubers do sprout the next year, provided that tubers
*       are present. Tubers are depleted up to 10% of their DW (per tuber).

    TWTUB = NDTUB* INTUB
    TWTUBD = NTUBD * INTUB

    IF (TWTUB .LE . 0.0)TWTUB = 0.

    IF (TWTUB .EQ. 0 .AND. DAY .EQ. 1)THEN
    WRITE(*,*)' There are no tubers !! -- Press <ENTER> '
    READ(*,*)
    STOP
    ENDIF

    IF (DVS .GE. 0.291 .AND. DVS .LT. 1.) THEN
          TWGTUB = INTGRL (TWGTUB,- REMOB,DELT)
          TWGTUB = AMAX1(0.0,TWGTUB)
      IF (NDTUB .GT. 0.) THEN
        REMOB  = TWGTUB * ROC * TEFF
      ENDIF
        IF (TWGTUB .LE. (0.01 * NPL * INTUB)) NGTUB = 0.0
    ELSE
          REMOB = 0.0
    ENDIF

*----New tuber formation takes place at DVS >1, daylength< 14.7 h, and 5 <water
*       temperature< 25 oC,provided plant wght > 0.1 g DW m-2; it continues until the
*       weight of that tuber class reaches the critical tuber weight equal to (number of
*       plants m-2)x(tuber number per plant)x (tuber weight per tuber)

        If (REMOB .EQ. 0.0) THEN
```

```
      If (DVS.GT.1.0 .AND. DAYL.LT.14.7)THEN
       If (DDTMP .GT. 5.0 .AND. DDTMP .LT. 25.0)THEN
        IF (TGW .GT .0.1) THEN
        NNTUB = NPL * NINTUB
        TRANS = AMAX1 (0.,(RTRL * (1./CVT) * (GPHOT-MAINT)))

         TWNTUB = INTGRL (TWNTUB, TRANS, DELT)
         ELSE
         TWNTUB = 0.0
         Endif

        IF (TWNTUB .GE. TWCTUB) THEN
*----When the new tuber class is finished, the new tubers are added to the total number of
*       dormant tubers
            NDTUB = NDTUB + (NPL * NINTUB)
            NTUBD = RDTU * NDTUB * TEFF

*----Reset new tuber number and weight back to zero
              NNTUB  = 0.0
              TWNTUB = 0.0
              ENDIF
       ELSE
       TRANS = 0.0
       ENDIF
      ELSE
      TRANS = 0.0
      ENDIF
     ELSE
     TRANS = 0.0
     ENDIF

*----Recalculate tuber numbers daily
       IF (DAY .GT. 1.0) THEN

*----NNTUB not added because they were included in NDTUB when reaching the total
*       critical dry weight of new tubers TWCTUB
        ENDIF

*----Dry matter and its partitioning over the plant organs
       TW   = TGW + (TWLVD + TWSTD + TWRTD)

       FLV = LINT(FLVT ,ILFLVT,DVS)
       FST = LINT(FSTT ,ILFSTT,DVS)
       FRT = LINT(FRTT ,ILFRTT,DVS)
       FL  = LINT(FLT  ,ILFLT ,DVS)

*----Growth of plant organs, maintenance respiration and translocation
      ASRQ = 1.46*FLV+1.51*FST+1.44*FRT
      MAINTS = 0.016*TWLVG+0.01*TWSTG+0.015*TWRTG
      MAINT  = MAINTS * TEFF
```

```
*----Sprouting tubers die if the resulting plant biomass has a negative net photosynthesis
*       during a user-defined number of consecutive days (23 is nominal). If this event
*       occurs, the program stops, and writes 'SURFAC'; By pressing enter, the program
*       continues ... KCOUNT is a counter variable, which counts the days with negative
*       net photosynthesis
      IF (GPHOT .LT. MAINT) THEN
        KCOUNT = KCOUNT + 1
      ELSE
        KCOUNT = 0
      ENDIF

      IF (KCOUNT.EQ.SSURPR .AND. SURFAC.LT.1.) THEN
         write(*,*)' KCOUNT = ',KCOUNT,'  SURFAC = ',SURFAC
         read(*,*)
        TWLVD = TWLVD + TWLVG
        TWSTD = TWSTD + TWSTG
        TWRTD = TWRTD + TWRTG

        TWLVG = 0.0
        TWSTG = 0.0
        TWRTG = 0.0
        REMOB = 0.0
        NDTUB = AMAX1 (0., NDTUB-NPL)

        IF (DVS .LT. 1.0. AND. NDTUB. GT. 0.) NGTUB = NPL

      ENDIF

*----Relative death rates
        RDR = INSW (DVS-2.001,0.,LINT (RDRT,ILRDRT,DAVTMP))
        RDS = INSW (DVS-2.001,0.,LINT (RDST,ILRDST,DAVTMP))

*----Development rates
      IF(DAVTMP .LT. 3.0) THEN
        DVR = 0.0
      ELSE IF (DVS.LE.1.) THEN
        DVR = 0.015*DAVTMP/30
      ELSE IF (DVS.GT.1.0 .AND. DVS .LT.20.0) THEN
        DVR = 0.040*DAVTMP/30
      ENDIF

*----Calculation of astronomic day length
      CALL ASTRO
     $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*----Daily temperature after 1 January, with base temperature
*       specified by user (given in MODEL.DAT)
        DTEFF = AMAX1(0.,DAVTMP-TBASE)

*----Calculation quantities dead plant material
        DLV   = TWLVG * RDR
        DST   = TWSTG * RDR
        DRT   = TWRTG * RDR
```

```
*----Shoot photosynthesis at light saturation and daytime temperature effect on shoot
*       photosynthesis
        AMAX   = AMAX1(0.00001,AMX * AMTMP)
        AMAX   = AMAX * REDAM
        AMTMP = LINT(AMTMPT,ILAMTM,DDTMP)

*----Before calling TOTASS, determine light extinction coefficients of plants (K) and of
*   water (L)
    L = LINT(LT,ILT,TIME)
    K = LINT(KT,IKT,DVS)

*----Daily total gross assimilation

        CALL TOTASS
   $    (SC,DAYL,SINLD,COSLD,DSINBE,RDD,RC,L,K,AMAX,EE,
   $    TL,DPT,RCSHST,TGW,FGROS,FL,FLV,FRT,FST,WLV,WST,
   $    DAY,HAR,HARDAY,HARDEP,DTGA,NPL,IRS,REMOB,TWLVG,
   $    TWSTG,TWRTG,SURFAC,CRIFAC)

*----If DVS is greater than one then REMOB should be set to zero
    IF (DVS .GE. 1.0) REMOB = 0.0

*----If harvesting takes place, weights various plant organs must be recalculated;
*       these are: TWLVG,TWSTG,TWRTG,TW)
        IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
        TWLVG = FLV * TGW
        TWSTG  = FST * TGW
        TWRTG = FRT * TGW
        TW    = TGW + (TWLVD + TWSTD + TWRTD)
    ENDIF

*----Conversion assimilated CO2 to CH2O
        GPHOT = DTGA * 30./44.

*----Total and net growth rates
        GTW = ((REMOB*CVT) + GPHOT - TRANS - MAINT) / ASRQ
        GRT = FRT * GTW
        GST = FST * GTW
        GLV = FLV * GTW

        NGLV = GLV - DLV
        NGST = GST - DST
        NGRT = GRT - DRT

*----Finish conditions
       IF (DVS.GT.20.0 .OR. DAY .EQ. 365.) TERMNL = .TRUE.

*----Output section
         IF (OUTPUT) THEN
         CALL OUTDAT (2,0,'DAVTMP ',DAVTMP)
         CALL OUTDAT (2,0,'DAYL    ',DAYL    )
         CALL OUTDAT (2,0,'DDTMP   ',DDTMP   )
         CALL OUTDAT (2,0,'DTEFF   ',DTEFF   )
         CALL OUTDAT (2,0,'DTGA    ',DTGA    )
```

```
      CALL OUTDAT (2,0,'DPT       ',DPT     )
      CALL OUTDAT (2,0,'DVS       ',DVS     )
      CALL OUTDAT (2,0,'FGROS     ',FGROS   )
      CALL OUTDAT (2,0,'GPHOT     ',GPHOT   )
      CALL OUTDAT (2,0,'IRS       ',IRS     )
      CALL OUTDAT (2,0,'MAINT     ',MAINT   )
      CALL OUTDAT (2,0,'NDTUB     ',NDTUB   )
      CALL OUTDAT (2,0,'NGTUB     ',NGTUB   )
      CALL OUTDAT (2,0,'NNTUB     ',NNTUB   )
      CALL OUTDAT (2,0,'NTM       ',NTM     )
      CALL OUTDAT (2,0,'NTUBD     ',NTUBD   )
      CALL OUTDAT (2,0,'REMOB     ',REMOB   )
      CALL OUTDAT (2,0,'TEFF      ',TEFF    )
      CALL OUTDAT (2,0,'TGW       ',TGW     )
      CALL OUTDAT (2,0,'TGWM      ',TGWM    )
      CALL OUTDAT (2,0,'TMPSUM',TMPSUM)
      CALL OUTDAT (2,0,'TRANS     ',TRANS   )
      CALL OUTDAT (2,0,'TREMOB ',TREMOB )
      CALL OUTDAT (2,0,'TW        ',TW      )
      CALL OUTDAT (2,0,'TWGTUB',TWGTUB )
      CALL OUTDAT (2,0,'TWLVD  ',TWLVD   )
      CALL OUTDAT (2,0,'TWLVG  ',TWLVG   )
      CALL OUTDAT (2,0,'TWNTUB',TWNTUB  )
      CALL OUTDAT (2,0,'TWRTD  ',TWRTD   )
      CALL OUTDAT (2,0,'TWRTG  ',TWRTG   )
      CALL OUTDAT (2,0,'TWSTD  ',TWSTD   )
      CALL OUTDAT (2,0,'TWSTG  ',TWSTG   )
      CALL OUTDAT (2,0,'TWTUB  ',TWTUB   )
      CALL OUTDAT (2,0,'TWTUBD',TWTUBD  )
      CALL OUTDAT (2,0,'WTMP   ',WTMP    )
      END IF

   ELSE IF (ITASK.EQ.3) THEN

*            INTEGRATION                *
*     ====================              *
      DVS    = INTGRL (DVS   ,DVR   ,DELT)
      TMPSUM = INTGRL (TMPSUM,DTEFF ,DELT)
      TREMOB = INTGRL (TREMOB,REMOB ,DELT)
      TWLVD  = INTGRL (TWLVD ,DLV   ,DELT)
      TWLVG  = INTGRL (TWLVG ,NGLV  ,DELT)
      TWLVG  = AMAX1 (0.0, TWLVG)
      TWSTD  = INTGRL (TWSTD ,DST   ,DELT)
      TWSTG  = INTGRL (TWSTG ,NGST  ,DELT)
      TWSTG  = AMAX1 (0.0, TWSTG)
      TWRTD  = INTGRL (TWRTD ,DRT   ,DELT)
      TWRTG  = INTGRL (TWRTG ,NGRT  ,DELT)
      TWRTG  = AMAX1 (0.0, TWRTG)
      NTUBPD = NTUBD
      NTUBD  = INTGRL (NTUBD, (RDTU*NDTUB*TEFF) ,DELT)
      NTUBD  = AMAX1 (0.0, NTUBD)
      NDTUB  = INTGRL (NDTUB, -(NTUBD-NTUBPD) ,DELT)
      NDTUB  = AMAX1 (0.0, NDTUB)
```

```
      ELSE IF (ITASK.EQ.4) THEN

*               TERMINAL SECTION                *
*               ================                *

*-----Terminal calculations

*-----Terminal output

      CLOSE (IUNITD)

      END IF

      ITOLD = ITASK

      RETURN
      END
*******************************************************************************************************
***                                        3.1 ASTRO                                                ***
*-------------------------------------------------------------------------------------------------------*
* SUBROUTINE ASTRO                                                                                      *
* Authors: Daniel van Kraalingen                                                                        *
* Date  : 9 August 1987                                                                                 *
* Modified by Jan Goudriaan 4 Febr 1988                                                                 *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                                           *
* Purpose: This subroutine calculates astronomic day length and  photoperiodic day length              *
* (see CABO-TPE report #?) and diurnal radiation characteristics such as daily integral of              *
* sine of solar elevation, solar constant. Measured daily total of global radiation is used            *
* to find atmospheric transmissivity and fraction diffuse radiation                                     *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                                       *
* name        meaning                                  units        class                            *
* -----       ---------                                ------       -----                            *
* DAY         Day number (Jan 1st = 1)                 -            I                                *
* LAT         Latitude of the site                     degrees      I                                *
* DTR         Measured daily total global radiation    J m-2 d-1    I                                *
* SC          Solar constant                           J m-2 s-1    O                                *
* DS0         Daily extraterrestrial radiation         J m-2 d-1    O                                *
* SINLD       Seasonal offset of sine of solar height  -            O                                *
* COSLD       Amplitude of sine of solar height        -            O                                *
* DAYL        Astronomical day length (base = 0 degrees) h          O                                *
* DSINB       Daily total of sine of solar height      s            O                                *
* DSINBE      Daily total of effective solar height    s            O                                *
*                                                                                                       *
* FATAL ERROR CHECKS (execution terminated, message) condition                                          *
*                                                                                                       *
* LAT > 67, LAT < -67                                                                                   *
*                                                                                                       *
* SUBROUTINES and FUNCTIONS called : none                                                               *
*                                                                                                       *
* FILE usage : none                                                                                     *
*-------------------------------------------------------------------------------------------------------*

      SUBROUTINE ASTRO (DAY,LAT,SC,DS0,SINLD,COSLD,
     $                  DAYL,DSINB,DSINBE)
```

```
      IMPLICIT REAL (A-Z)

*----PI and conversion factor from degrees to radians
      PARAMETER (PI=3.141592654, RAD=0.017453292)

*----Check on input range of parameters
      IF (LAT.GT.67.)  STOP 'ERROR IN ASTRO: LAT > 67'
      IF (LAT.LT.-67.) STOP 'ERROR IN ASTRO: LAT <-67'

*----Declination of the sun as function of daynumber (DAY)
      DEC = -ASIN(SIN(23.45*RAD)*COS(2.*PI*(DAY+10.)/365.))

*----SINLD, COSLD and AOB are intermediate variables
      SINLD = SIN(RAD*LAT)*SIN(DEC)
      COSLD = COS(RAD*LAT)*COS(DEC)
      AOB   = SINLD/COSLD

*----Daylength (DAYL)
      DAYL  = 12.0*(1.+2.*ASIN(AOB)/PI)

      DSINB = 3600.*(DAYL*SINLD+24.*COSLD*SQRT(1.-AOB*AOB)/PI)
      DSINBE= 3600.*(DAYL*(SINLD+0.4*(SINLD*SINLD+COSLD*COSLD*0.5))+
     $      12.0*COSLD*(2.0+3.0*0.4*SINLD)*SQRT(1.-AOB*AOB)/PI)

*----Solar constant (SC) and daily extraterrestrial (DS0)
      SC  = 1370.*(1.+0.033*COS(2.*PI*DAY/365.))
      DS0 = SC*DSINB
      RETURN
      END
```

3.2 TOTASS

```
* SUBROUTINE TOTASS                                                              *
* Authors: Daniel van Kraalingen                                                 *
* Date   : 1 December 1987                                                       *
* Modified by Jan Goudriaan 5-Febr-1988                                          *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                    *
* Units modified by Elly Best & Will Boyd 28 July 1995                           *
*   Purpose: This subroutine calculates daily total gross  assimilation (DTGA) by *
*   performing a Gaussian integration over time. At three different times of the day,*
*   radiation is computed and used to determine assimilation whereafter integration*
*   takes place (Source: Post-graduate Course 'Simulation of plant growth and crop *
*   production. Pontignano, Siena, Italy;  3-12 November, 1992. Dept. Theor.      *
*   Production Ecol.  (TPE-WAU), Wageningen Agricultural University, and DLO-Centre*
*   for Agrobiological Research (CABO-DLO).)                                     *
*                                                                                *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                *
* name       meaning                                    units      class       *
* ------     ---------                                  ------     ------      *
* SC         Solar constant                             J m-2 s-1  I           *
* DAYL       Day length (base = 0 degrees)              h          I           *
* SINLD      Intermediate variable in calculating solar declination  -          I           *
* COSLD      Intermediate value in calculating solar height  -          I           *
* DSINBE     Daily total of effective solar height      s          I           *
```

```
* DTR       Measured daily total of global radiation                  J m-2 d-1  I    *
* RC        Reflection coefficient of irradiation at water surface (relative)  -     I    *
* L         Water type specific light extinction coefficient          -          I    *
* K         Plant species specific light extinction coefficient       -          I    *
* AMAX      Assimilation rate at light saturation for individual shoots  g CO2/g DW/h  I  *
* EE        Initial light use efficiency for individual shoots        g CO2 J-1  I    *
* TL        Thickness per plant layer                                 m          I    *
* DPT       Water depth                                               m          I    *
* RCHSHST   Relation coefficient shoot weight-stem length             m g DW-1   I    *
* TGW       Total live plant dry weight                               g DW m-2   I    *
* FGROS     Instantaneous assimilation rate of whole canopy           g CO2/m2 soil/h  O  *
* FL        Leaf dry matter allocation to each layer of  plant        -          I    *
* FLV       Fraction of total dry matter increase allocated to leaves  -         I    *
* FRT       Fraction of total dry matter increase allocated to roots  -          I    *
* FST       Fraction of total dry matter increase allocated to stems  -          I    *
* WLV       Dry weight of leaves                                      g DW m-2   I    *
* WST       Dry weight of stems                                       g DW m-2   I    *
* HAR       Harvesting                                                -          I    *
* HARDAY    Harvesting day number                                     d          I    *
* HARDEP    Harvesting depth                                          m          I    *
* DTGA      Daily total gross assimilation                            g CO2 m-2 d-1  O  *
* NPL       Plant density                                             plants m-2 I    *
* IRS       Total irradiance just under the water surface             J m-2 s-1  I    *
* REMOB     Remobilization rates of carbohydrates                     g DW m-2 d-1 I  *
* TWLVG     Total dry weight of live leaves                           g DW m-2   I    *
* TWSTG     Total dry weight of live stems                            g DW m-2   I    *
* TWRTG     Total dry weight of live roots                            g DW m-2   I    *
* SURFAC    Expression of warning that plant canopy is not at         -               *
*           surface and tuber class has died                                          *
* CRIFAC    Critical weight per 0.1 m plant layer                     gDW/0.1 m  I    *
*                                                                     plnt ht per plnt *
*                                                                                      *
* SUBROUTINES and FUNCTIONS called : ASSIM                                             *
*                                                                                      *
* FILE usage : none                                                                    *
*--------------------------------------------------------------------------------------*

      SUBROUTINE TOTASS (SC,DAYL,SINLD,COSLD,DSINBE,DTR,RC,L,K,
     $                   AMAX,EE,TL,DPT,RCSHST,TGW,FGROS,FL,
     $                   FLV,FRT,FST,WLV,WST,DAY,HAR,HARDAY,
     $                   HARDEP,DTGA,NPL,IRS,REMOB,TWLVG,TWSTG,
     $                   TWRTG,SURFAC,CRIFAC)

      IMPLICIT REAL(A-Z)
      REAL XGAUSS(3), WGAUSS(3)
      INTEGER II, IGAUSS

      PARAMETER (PI=3.141592654)

      DATA IGAUSS /3/
      DATA XGAUSS /0.1127, 0.5000, 0.8873/
      DATA WGAUSS /0.2778, 0.4444, 0.2778/

*-----Assimilation set to zero & three different times of the day (HOUR)
```

```
      DTGA = 0.
      DO 10 II=1,IGAUSS

*-----At the specified HOUR, radiation is computed and used to compute assimilation
      HOUR = 12.0+DAYL*0.5*XGAUSS(II)

*-----Sine of solar elevation
      SINB  = AMAX1(0.,SINLD+COSLD*COS(2.*PI*(HOUR+12.)/24.))

*-----Diffuse light fraction (FRDIF) from atmospheric transmission  (ATMTR)
      PAR    = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      ATMTR  = PAR/(0.5*SC*SINB)
      FRDIF  = 1.47-1.66*ATMTR
      IF (ATMTR.LE.0.35.AND.ATMTR.GT.0.22) FRDIF=1.-6.4*(ATMTR-0.22)**2
      IF (ATMTR.LE.0.22) FRDIF=1.
      FRDIF  = AMAX1(FRDIF,0.15+0.85*(1.-EXP(-0.1/SINB)))

*-----Diffuse PAR (PARDIF) and direct PAR (PARDIR)
      PAR    = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      PARDIF =  MIN (PAR,SINB*FRDIF*ATMTR*0.5*SC)
      PARDIR = PAR-PARDIF

      CALL ASSIM
     $ (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,DPT,RCSHST,TGW,
     $ FL,FLV,FRT,FST,WLV,WST,DAY,HAR,HARDAY,HARDEP,II,FGROS,NPL,IRS,
     $ REMOB,TWLVG,TWSTG,TWRTG,SURFAC,CRIFAC)

*-----Integration of assimilation rate to a daily total (DTGA)
      DTGA = DTGA+FGROS*WGAUSS(II)
10    CONTINUE

      DTGA = DTGA*DAYL

      RETURN
      END
```

****

*** 3.3 ASSIM ***

*

* Authors: Elly Best & Will Boyd
* Date : 28 July 1999
* Purpose: This subroutine performs a momentaneous calculation of light profile
* in the water column, light absorbed by the available for photosynthesis, and
* assimilation at all these depth layers. The depth-integrated variable is FGROS. At
* harvesting, the plant material is removed per depth layer from the existing biomass
*

* FORMAL PARAMETERS: (I=input,O=output,C=control,IN=init,T=time)

* name	meaning	units	class
* PARDIR	Instantaneous flux of direct radiation (PAR)	W m-2	I
* PARDIF	Instantaneous flux of diffuse radiation(PAR)	W m-2	I
* RC	Reflection coeff. of irradiation at water surf. (relative)	-	I
* L	Water type specific light extinction coefficient	m-2	I

```
* K         Plant species specific light extinction coefficient          m2 g-1DW   I     *
* AMAX      Assimilation rate at light saturation for individual shoots  g CO2/g DW/h I     *
* EE        Initial light use efficiency for individual shoots             g CO2 J-1  I     *
* TL        Thickness per plant layer                                      m          I     *
* DPT       Water depth                                                    m          I     *
* RCHSHST   Relation coefficient tuber weight-stem length                  m/g DW     I     *
* TGW       Total live plant dry weight                                    g DW m-2   I     *
* FL        Leaf dry matter allocation to each layer of plant              -          I     *
* FLV       Fraction of total dry matter incr. allocated to leaves         -          I     *
* FRT       Fraction of total dry matter incr. allocated to roots          -          I     *
* FST       Fraction of total dry matter incr. allocated to stems          -          I     *
* WLV       Dry weight of leaves                                           g DW m-2   I     *
* WST       Dry weight of stems                                            g DW m-2   I     *
* HAR       Harvesting                                                     -          I     *
* HARDAY    Harvesting day number                                          d          I     *
* HARDEP    Harvesting depth                                               m          I     *
* II        Counter in DO LOOP, indicates 1 of 3 x p.d.(HOUR)              -          I     *
* FGROS     Instantaneous assimilation rate of the plant                   g CO2/m2/h O     *
* NPL       Plant density                                                  plants m-2 I     *
* IRS       Total irradiance just under the water surface                  J m-2 s-1  I     *
* REMOB     Remobilization rates of carbohydrates                          g DW m-2 d-1 I   *
* TWLVG     Total dry weight of live leaves                                g DW m-2   I     *
* TWSTG     Total dry weight of live stems                                 g DW m-2   I     *
* TWRTG     Total dry weight of live roots                                 g DW m-2   I     *
* SURFAC    Expression of warning that plant canopy is not at              -                *
*           surface and tuber class has died                                                *
* CRIFAC    Critical weight per 0.1 m plant layer                          gDW/0.1 m  I     *
*                                                                          plnt ht per plnt *
*                                                                                           *
* SUBROUTINES called : none                                                                 *
* FUNCTIONS called : AFGEN                                                                  *
*                                                                                           *
* FILE usage : none                                                                         *
*-------------------------------------------------------------------------------------------*

      SUBROUTINE ASSIM (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,
     $                  DPT,RCSHST,TGW,FL,FLV,FRT, FST,
     $                  WLV,WST,DAY,HAR,HARDAY,HARDEP,II,
     $                  FGROS,NPL,IRS,REMOB,TWLVG,TWSTG,
     $                  TWRTG,SURFAC,CRIFAC)

      IMPLICIT REAL(A-Z)
      REAL DMPC(5), SC(100), IRZ(100) , IABS(100), IABSL(100)
      REAL HIG(100), AH(100), REDF(100), SumZ, SumZ1, SumZ2
      INTEGER IMN1, IRED, I, LOOP, Layers, ILAY, II, MM
      INTEGER SLayer
      PARAMETER (IMN1  = 40)
      REAL REDFT(IMN1), DMPCT(IMN1)

*----Read AFGEN functions
      CALL RDAREA ('REDFT ',REDFT ,IMN1  ,IRED  )
      CALL RDAREA ('DMPCT ',DMPCT, IMN1  ,ILAY  )
```

```
*----Irradiation just beneath the water surface
      IRS = PARDIR + PARDIF
      IRZ(1) = IRS * (1.0 - RC)

*----Set a critical shoot weight for each depth layer
      CRIGWT = CRIFAC * NPL

*----Canopy assimilation is set to zero
      FGROS = 0.

*----Calculate stem length
      STEMLE = AMIN1(DPT+.0995, (RCSHST*(WLV+WST)))

*----Calculate shoot biomass
      SHTBIO = TWLVG + TWSTG

      IF (STEMLE .GT. DPT+.08)THEN

*----Determine total number of layers in the given water depth
      LOOP = INT (DPT/TL + 0.1) + 1

*----Water depth must be > or = 0.5m to use this distribution
*     method; otherwise, go to ELSE which will distribute biomass equally
      IF (LOOP .GE. 6) THEN

*----If the biomass per layer is>or = the critial weight, proceed as usual
      IF ((SHTBIO/(MIN(LOOP-1,12))) .GE. CRIGWT) THEN

*----Since plant biomass has either reached the surface or reached its maximum height,
*          REMOB becomes zero
      REMOB = 0.0
      SURFAC = 1.

*----Initialize variable to sum percent biomass in bottom 5 layers
      BOTM5 = BOTM5 + DMPC(I)

*----Distribute the DMPC-specified share of total biomass in botoom 5 layers-
*          exclude last layer, because this layer has been reserved for roots
      DO 10  I = 1,5
      VAL = REAL (I)
      DMPC(I) = LINT (DMPCT, ILAY, VAL)

*----Sum of percent biomass found in bottom 5 layers
      BOTM5 = BOTM5 + DMPC(I)
      SC(LOOP-I) = TGW * DMPC(I)

   10 CONTINUE

*----Determine the percent biomass distributed over the upper layers
      PCTUP = 1.0 - (BOTM5 + FRT)

*----Distribute the DMPC-specified share of (nominal=78%) total biomass in
*     bottom 5 layers-exclude last layer because this layer has been reserved for roots
**       write(*,*)' Total weight = ',TGW
```

```
      DO 10 I = 1,5
      VAL = REAL (I)
      DMPC(I) = LINT (DMPCT,ILAY,VAL)
      SC(LOOP-I) = TGW * DMPC(I)
**      write(*,*)' layer ',I,' = ',SC(I)
   10 CONTINUE

*----Distribute the percent biomass over the upper layers
*      with biomass distributed evenly toward the top
*      LOOP (integer) .. Number of 0.1m water layers
*      LAYERS (integer) .. Layers remaining after bottom 5 & roots
*      SLAYER (integer) .. Layers above the 1.2m water depth
*      SUMZ1 (real) .. Summation of layers 1 through LOOP-6
*      SUMZ2 (real) .. Summation of layers 1 throgh LOOP-13
*----SUMZ (real) .. Difference between SUMZ1 and SUMZ2

*----6 Is the bottom 5 layers + the bottom 1 layer (roots)

      LAYERS = LOOP - 6
      SUMZ1 = (LAYERS/2.0) * (LAYERS+1)
      SLAYER = MAX(0,LOOP-13)
      SUMZ2 = (SLAYER/2.0) * (SLAYER+1)
      SUMZ = SUMZ1 - SUMZ2

      IF (LOOP .GT. 6)THEN
      DO 20 I = LOOP-6, MAX(LOOP-12,1),-1
      SC(I) = I/SUMZ * (TGW * PCTUP)
   20 CONTINUE
      ENDIF
*----If the biomass per layer<critical weight, take away layers until enough
      ELSE

      LESS = 1
   23 LESS =   LESS + 1

*----Initialize all layers at 0.0
      DO 25 MM = 1,LOOP-1
        SC(MM) = 0.0
   25 CONTINUE

*----If critical biomass is not met ... go back to 23 & remove a layer
      IF (SHTBIO/(LOOP-LESS).LT.CRIGWT .AND. LOOP-LESS.GT.1)GOTO 23

*----Otherwise distribute shoot biomass over the layers it can reach
*----Loop goes from bottom to top ... i.e. 10,9,8, ...,2,1
      SURFAC = 0.
      IF ((LOOP-1)-LESS .LE. 12)THEN

*----The above IF,THEN stops the process if depth > 1.2 meters
      DO 27 MM = LOOP-1,LESS,-1
        SC(MM) = AMIN1(CRIGWT, SHTBIO)
        IF (SHTBIO .GT. CRIGWT) SC(MM-1) = SHTBIO - CRIGWT
        IF (SHTBIO .GT. CRIGWT) SHTBIO = SHTBIO - CRIGWT
   27 CONTINUE
      ENDIF
```

```
      ENDIF

      ELSE

*----If water depth is 0.5m or less, plant biomass is distributed  evenly over the existing
*          layers
*----If biomass reaches the surface ... proceed as usual
      IF (SHTBIO/(LOOP-1) .GE. CRIGWT) THEN
      SURFAC = 1.
      DO 32 I = 1,LOOP-1
      SC(I) = SHTBIO/(LOOP-1)
**      write(*,*)' layer ',I,' = ',SC(I)
   32 CONTINUE

      ELSE

*----If biomass does not reach the surface
      LESS = 1
   33 LESS = LESS + 1

*----Initialize all layers at 0.0
      DO 35 MM = 1,LOOP-1
        SC(MM) = 0.0
   35 CONTINUE

*----If critical biomass is not met ... go back to 33 & remove a layer
      IF ((SHTBIO/(LOOP-LESS)).LT.CRIGWT .AND. LOOP-LESS.GT.1)GOTO 33

*----Otherwise distribute shoot biomass over the layers it can reach
*----Loop goes from bottom to top ... i.e. 8,7,6, ...,2,1
      SURFAC = 0.
      DO 37 MM = LOOP-1,LESS,-1
        SC(MM) = AMIN1(CRIGWT, SHTBIO)
        IF (SHTBIO .GT. CRIGWT) SC(MM-1) = SHTBIO - CRIGWT
        IF (SHTBIO .GT. CRIGWT) SHTBIO = SHTBIO - CRIGWT
   37 CONTINUE

      ENDIF

      ENDIF

*----Distribute 12.3% of biomass in the last layer (roots)
      SC(LOOP) = TGW * FRT
**      write(*,*)' layer ',LOOP,' = ',SC(LOOP)
**      read(*,*)

*----Harvesting
      IF (HAR .EQ. 1. .AND. DAY .EQ. HARDAY)THEN
      IF (HARDEP .GT. DPT) HARDEP = DPT
      DO 45 I = 1,(HARDEP/.1 + 1.0)
      SC(I) = 0.0
   45 CONTINUE
```

```
*-----Reset total live weight (TGW) to zero
      IF(II .EQ. 1)TGW = 0.0
      ENDIF

      DO 60 I = 1,LOOP

*-----Total irradiation on top of stratum I
      IRZ(I+1) = IRZ(I) * EXP(-TL* L - K* SC(I))
      IF(SC(I) .EQ. 0.0) GOTO 48

*-----Radiation absorbed by macrophyte community
      IABS(I) = (IRZ(I)-IRZ(I+1))*SC(I)*K/(K*SC(I)+TL*L)

*-----Radiation absorbed by leaves, excluding bottom layer
      IF(I .LT. LOOP) IABSL(I) = IABS(I) * FL
      IF(IABSL(I) .EQ. 0.0)GOTO 48

*-----Height on top of stratum I measured from the water surface
      HIG(I) = TL * (LOOP - I)

*-----Absolute height of vegetation on top of stratum I, measured
*          from the top of the plant
      AH(I) = STEMLE - HIG(I)

*-----Reduction factor over the vertical of the vegetation
      REDF(I) = LINT(REDFT,IRED,AH(I))

*-----Instantaneous CO2 assimilation rate per depth layer
      FGL = SC(I)*AMAX*REDF(I)*(1.-EXP(-EE*IABSL(I)*3600. /
     $ (AMAX*REDF(I)*SC(I))))
      GOTO 50
   48 FGL = 0.0
   50 FGROS = FGROS + FGL

*-----If plants are harvested, live plant weight is recalculated
      IF (HAR.EQ.1 .AND. DAY.EQ.HARDAY .AND. II.EQ.1) THEN
      TGW = TGW + SC(I)
      ENDIF
   60 CONTINUE
      ENDIF

      RETURN
      END
```

```
*-----------------------------------------------------------------------------*
* MODEL.DAT file                                                              *
* contains:                                                                   *
* - Initial constants as far as specified with INCON statements,              *
* - Model parameters,                                                         *
* - AFGEN functions,                                                          *
* - A SCALE array in case of a general translation                            *
*                                                                             *
* File name: MODELVC.DAT; input MODEL.DAT file for calibration run of VALLA   *
* Calibration data cf. Titus & Stephens, 1983; weather file USA6.978 pertaining*
*   to Binghamton, NY, 1978.                                                  *
* Date: 10 August 99                                                          *
*Time: 14:00:00                                                               *
*-----------------------------------------------------------------------------*

* Initial constants
* -----------------
INTUB    = 0.09
IREMOB   = 0.
IWLVD    = 0.
IWLVG    = 0.
IWRTD    = 0.
IWRTG    = 0.
IWSTD    = 0.
IWSTG    = 0.
NUL      = 0.
REMOB    = 0.0

* Model parameters
* ----------------
YRNUM    = 1.
AMX      = 0.0165
CRIFAC   = 0.0091
CVT      = 1.05
DAYEM    = 1.
DELAY    = 1.
EE       = 0.000011
HAR      = 0.
HARDAY   = 304.
HARDEP   = 0.8
NDTUB    = 233.
NINTUB   = 5.5
NPL      = 30.
RC       = 0.06
RCSHST   = 12.0
RDTU     = 0.018
REDAM    = 1.
ROC      = 0.0576
RTR      = .247
SURPER   = 23.
TBASE    = 3.
TL       = 0.1
TWCTUB   = 14.85
```

```
* AFGEN functions
* ----------------------
* AMDVST =
*   0.001, 1.,
*   1.243, 1.,
*   1.244, 0.6,
*   20.0, 0.6

AMTMPT =
   -30., 0.00001,
   0., 0.00001,
   5., 0.12,
   15., 0.424,
   20., 0.568,
   25., 0.735,
   30., 0.879,
   35., 1.0,
   50., 0.00001

DMPCT  =
   1.0, .184,
   2.0, .184,
   3.0, .184,
   4.0, .114,
   5.0, .114

DPTT=
    1., 1.4,
    365., 1.4

* DVRVT   =
*  -15., 0.,
*    0., 0.,
*   30.,0.015
* DVRRT   =
*  -15., 0.,
*    0., 0.,
*   30.,0.040

FLT    =
   0., 0.82,
   3.5, 0.82,
   20.0, 0.82

 FLVT   =
   0., 0.718,
   3.5, 0.718,
   20.0, 0.718

FSTT   =
   0., 0.159,
   3.5, 0.159,
   20.0, 0.159
```

```
FRTT  =
   0., 0.123,
   3.5, 0.123,
   20.0, 0.123

KT    =
   0., 0.0235,
   3.5, 0.0235,
   20.0, 0.0235

LT    =
   1., 0.43,
   7., 0.43,
   28., 0.43,
   35., 0.43,
   57., 0.43,
   63., 0.43,
   68., 0.43,
   77., 0.43,
   84., 0.43,
   91., 0.43,
   99., 0.43,
   105., 0.43,
   112., 0.43,
   121., 0.43,
   135., 0.80,
   153., 0.49,
   158., 0.60,
   166., 0.47,
   178., 0.45,
   188., 0.47,
   199., 0.50,
   222., 0.57,
   225., 0.59,
   243., 0.50,
   250., 0.43,
   266., 0.43,
   270., 0.43,
   274., 0.43,
   280., 0.43,
   284., 0.43,
   290., 0.43,
   294., 0.43,
   298., 0.43,
   301., 0.43,
   305., 0.43,
   310., 0.43,
   320., 0.43,
   330., 0.43,
   365., 0.43

RDRT  =
   0., 0.021,
```

```
   19., 0.021,
   30., 0.042,
   40., 0.084,
   50., 1.

RDST  =
   0., 0.021,
   19., 0.021,
   30., 0.042,
   40., 0.084,
   50., 1.

REDFT  =
   0.0, 1.0,
   1.0, 1.0,
   20.0, 1.0

TEFFT  =
   0.0, 0.0001,
   10., 0.5,
   20., 1.,
   30., 2.,
   40., 4.,
   45., 6.,
   50., 0.0001

WTMPT  =
   1.,  5.5,
   7.,  5.5,
   14., 5.5,
   28., 5.5,
   35., 5.5,
   42., 5.5,
   49., 5.5,
   57., 5.5,
   63., 5.5,
   68., 5.5,
   77., 5.5,
   84., 5.5,
   91., 5.5,
   95., 5.5,
   135., 13.,
   153., 23.,
   156., 21.,
   158., 16.,
   162., 19.,
   166., 18.,
   174., 21.,
   178., 22.,
   188., 21.,
   194., 20.,
   199., 21.,
   210., 22.,
   220., 22.,
```

```
   227., 25.,
   243., 20.,
   250., 20.,
   258., 16.,
   266., 15.,
   305., 5.5,
   310., 5.5,
   315., 5.5,
   320., 5.5,
   325., 5.5,
   330., 5.5,
   335., 5.5,
   365., 5.5

NTMT  =
   1., 233.,
  98., 233.,
  134., 233.,
  162., 233.,
  190., 233.,
  233., 233.,
  260., 233.,
  289., 233.,
  365., 233.

TGWMT  =
   1., 0.,
  153., 2.4,
  166., 3.8,
  178., 7.1,
  199., 17.3,
  220., 50.1,
  243., 41.0,
  266., 25.3,
  365., 0.
```

```
*_____________________________________________________________________*
* TIMER file contains                                                  *
*                                                                      *
* - The used DRIVER and TRACE in case of GENERAL translation           *
* - The TIMER variables used in both translation modes                 *
* - Additional TIMER variables in case of GENERAL translation          *
* - The WEATHER control variables if weather data are used             *
* - Miscellaneous FSE variables in case of FSE translation             *
*                                                                      *
* File: VALLA.FOR                                                      *
* Date: 09-08-97                                                       *
* Time: 15:40:06                                                       *

 * TIMER variables used in GENERAL and FSE translation modes          *
* _____________________________________________________________________*
 STTIME      = 1.    ! start time
 FINTIM      = 365.  ! finish time
 DELT        = 1.    ! time step (for Runge-Kutta first guess)
 PRDEL       = 1.    ! output time step
 IPFORM      = 4     ! code for output table format:
                     ! 4 = spaces between columns
                     ! 5 = TAB's between columns (spreadsheet output)
                     ! 6 = two column output

                     ! The string array PRSEL contains the output variables for which
                     ! formatted tables have to be made. One or more times there is a
                     ! series of variable names terminated by the word <TABLE>.
                     ! The translator writes the variables in each PRINT statement to
 PRSEL       =       ! a separate table.
* 'DAVTMP',
* 'DAYL  ',
* 'DDTMP ',
* 'DTEFF ',
* 'DTGA  ',
* 'DVS   ',
* 'FGROS ',
* 'GPHOT ',
* 'IRS   ',
* 'MAINT ',
  'NDTUB ',
* 'NGTUB ',
* 'NNTUB ',
* 'NTM   ',
* 'NTUBD ',
* 'NTUBPD',
* 'REMOB ',
*  'TEFF  ',
  'TGW   ',
* 'TGWM  ',
* 'TMPSUM',
* 'TRANS ',
* 'TREMOB',
* 'TW    ',
```

```
* 'TWGTUB',
* 'TWLVD ',
* 'TWLVG ',
* 'TWNTUB',
* 'TWRTD ',
 'TWRTG ',
* 'TWSTD ',
* 'TWSTG ',
* 'TWTUB ',
* 'TWTUBD',
*'WTMP ',
      '<TABLE>'
 COPINF = 'N'        ! Switch variable whether to copy the input files
                     ! to the output file ('N' = do not copy,
                     ! 'Y' = copy)
 DELTMP = 'N'        ! Switch variable what should be done with the
                     ! temporary output file ('N' = do not delete,
                     ! 'Y' = delete)
 IFLAG  = 1101       ! Indicates where weather error and warnings
                     ! go (1101 means errors and warnings to log
                     ! file, errors to screen, see FSE manual)
*IOBSD = 1991,182    ! List of observation data for which output is
                     ! required. The list should consist of pairs
                     ! <year>,<day> combination

* WEATHER control variables
* ------------------
 WTRDIR      = 'C:\SYS\WEATHER\'
 CNTR        = 'USA'       ! Country code
 ISTN        = 6           ! Station code
 IYEAR       = 1978        ! Year
```

```
*-------------------------------------------------------------------------------*
* CONTROL.DAT file contains:                                                    *
* File names to be used by FSE 2.1                                              *
* The input files (except FILEIR) may be used in reruns.                        *
* Up to five input data files may be used (FILEI1-5)                            *
*-------------------------------------------------------------------------------*

  FILEON = 'RES.DAT'          ! Normal output file
  FILEOL = 'MODEL.LOG'        ! Log file
  FILEIR = 'RERUNS.DAT'       ! Reruns file
  FILEIT = 'TIMER.DAT'        ! File with timer data
  FILEI1 = 'MODEL.DAT'        ! First input data file

* FILEI2 = ' '                ! Second input data file (not used)
* FILEI3 = ' '                ! Third input data file (not used)
* FILEI4 = ' '                ! Fourth input data file (not used)
* FILEI5 = ' '                ! Fifth input data file (not used)
```

Appendix B
Variable Listing

Abbreviation	Explanation	Dimension
AH(i)	Absolute height of vegetation on top of stratum I, measured from the plant top	m
AMAX	Actual CO_2 assimilation rate at light saturation for individual shoots	g CO_2.g DW^{-1}.h^{-1}
AMTMP	Daytime temperature effect on AMX (relative)	-
AMTMPT	Table of AMX as function of DVS	-, -
AMX	Potential CO_2 assimilation rate at light saturation for shoot tips	g CO_2.g DW^{-1}.h^{-1}
ASRQ	Assimilate requirement for plant dry matter production	g CH_2O.g DW^{-1}
ATMTR	Atmospheric transmission coefficient	-
COSLD	Intermediate variable in calculating solar height	-
CRIFAC	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}. $plnt^{-1}$
CRIGWT	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}. m^{-2}
CVT	Conversion factor of translocated dry matter into CH_2O	-
DAVTMP	Daily average temperature	°C
DAY	Day number (January 1=1)	d
DAYEM	First Julian day number	d
DAYL	Day length	h
DDELAY	Integer value of DELAY	-
DDTMP	Daily average daytime temperature	°C
DEC	Declination of the sun	radians
DELAY	Lag period chosen to relate water temperature to air temp., in cases where water temp. has not been measured	d
DEPTH	Water depth	m
DLV	Death rate of leaves	g DW. m^{-2}.d^{-1}
DMPC(i)	Dry matter allocation to each plant layer (relative)	-
DMPCT	Table to read DMPC(i) as function of depth layer (relative)	-
DPTT	Table to read water depth as a function of day no	m, d
DRT	Death rate of roots	g DW. m^{-2}.d^{-1}
DSINB	Integral of SINB over the day	s.d^{-1}
DSINBE	Daily total of effective solar height	s.d^{-1}
DSO	Daily extra-terrestrial radiation	J.m^{-2}.d^{-1}
DST	Death rate of stems	g DW.m^{-2}.d^{-1}
DTEFF	Daily effective temperature	°C
DTGA	Daily total gross CO_2 assimilation of the vegetation	g CO_2.m^{-2}.d^{-1}
DTR	Measured daily total global radiation	J.m^{-2}.d^{-1}
DVR	Development rate as function of temperature sum	d^{-1}
DVRRT	Table of post-anthesis development rate as function of temperature sum (used for calibration; not read from MODEL.DAT)	d^{-1}, °C
DVRVT	Table of pre-anthesis development rate as function of temperature sum (used for calibration; not read from MODEL.DAT)	d^{-1}, °C
DVRVT	Development rate pre-anthesis	d-1
DVS	Development phase of the plant	-
EE	Initial light use efficiency for shoots	g CO_2 . J^{-1}
FGROS	Instantaneous CO_2 assimilation rate of the vegetation	g CO_2.m^{-2}.h^{-1}
FGL	Instantaneous CO_2 assimilation rate per vegetation layer	g CO_2.m^{-2}.h^{-1}

FL	Leaf dry matter allocation to each layer of shoot (relative)	-
FLT	Table to read FL as function of DVS	-, -
FLV	Fraction of total dry matter increase allocated to leaves	-
FLVT	Table to read FLV as function of DVS	-
FRDIF	Diffuse radiation as a fraction of total solar radiation	-
FRT	Fraction of total dry matter increase allocated to roots	-
FRTT	Table to read FRT as function of DVS	-, -
FST	Fraction of total dry matter increase allocated to stems	-
FSTT	Table to read FST as function of DVS	-, -
GLV	Dry matter growth rate of leaves	g DW.m-2.d-1
GPHOT	Daily total gross assimilation rate of the vegetation	g $CH_2O.m^{-2}.d^{-1}$
GRT	Dry matter growth rate of roots	g $DW.m^{-2}.d^{-1}$
GST	Dry matter growth rate of stems	g $DW.m^{-2}.d^{-1}$
GTW	Dry matter growth rate of the vegetation (plant excluding Tubers)	g $DW.m^{-2}.d^{-1}$
HAR	Harvesting (0=no harvesting, 1=harvesting)	-
HARDAY	Harvesting day number	d
HARDEP	Harvesting depth (measured from water surface)	m
HIG(i)	Height on top of stratum I (measured from water surface)	m
HOUR	Selected hour during the day	h
I	Counter in DO LOOP	-
IABS(i)	Total irradiance absorbed per depth layer	$J.m^{-2}.s^{-1}$
IABSL(i)	Total irradiance absorbed per depth layer	$J.m^{-2}.s^{-1}$
IDAY	Integer equivalent of variable DAY	d
INTUB	Initial dry weight of a tuber	g $DW.tuber^{-1}$
IREMOB	Initial value remobilization	g $CH_2O.m^{-2}$
IRS	Total irradiance just under the water surface	$J.m^{-2}.s^{-1}$
IRZ(i)	Total irradiance on top of depth layer I	$J.m^{-2}.s^{-1}$
IWLVD	Initial dry matter of dead leaves	g $DW.m^{-2}$
IWLVG	Initial dry matter of green (live) leaves	g $DW.m^{-2}$
IWRTD	Initial dry matter of dead roots	g $DW.m^{-2}$
IWRTG	Initial dry matter of green (live) roots	g $DW.m^{-2}$
IWSTD	Initial dry matter of dead stems	g $DW.m^{-2}$
IWSTG	Initial dry matter of green (live) stems	g $DW.m^{-2}$
K	Plant species specific light extinction coefficient	$m^2.g\ DW^{-1}$, -
KCOUNT	Counter used to calculate number of consecutive days in which seedlings have a negative net photosynthesis	-
KT	Table to read K as function of DVS	-
L	Water type specific light extinction coefficient	m^{-1}
LAT	Latitude of the site	degrees
LT	Table to read L as function of day number	d, m^{-1}
MAINT	Maintenance respiration rate of the vegetation	g $CH_2O.m^{-2}.d^{-1}$
MAINTS	Maintenance respiration rate of the vegetation at reference temperature	g $CH_2O.m^{-2}.d^{-1}$
NDTUB	Dormant tuber number	dormant $tubers.m^{-2}$
NGLV	Net growth rate of leaves	g $DW.m^{-2}.d^{-1}$
NGRT	Net growth rate of roots	g $DW.m^{-2}.d^{-1}$
NGST	Net growth rate of stems	g $DW.m^{-2}.d^{-1}$
NGTUB	Sprouting tuber number	spr. $tubers.m^{-2}$
NINTUB	Tuber number concurrently initiated per plant	conc.in.tubers $.plnt^{-1}$
NNTUB	New tuber number	new $tubers.m^{-2}$
NPL	Plant density	$plants.m^{-2}$
NTM	Tuber density measured (field site)	$tubers.m^{-2}$

NTMT	Table to read NTM as function of day number	tubers.m^{-2}, d
NTUBD	Dead tuber number	dead tubers.m^{-2}
NUL	Zero (0)	-
NTUBPD	Dead tuber number previous day	dead p.d.tubers.m^{-2}
PAR	Instantaneous flux of photosynthetically active radiation	J.m^{-2}.s^{-1}
PARDIF	Instantaneous flux of diffuse PAR	J.m^{-2}.s^{-1}
PARDIR	Instantaneous flux of direct PAR	J.m^{-2}.s^{-1}
PI	Ratio of circumference to diameter of circle	-
RAD	Factor to convert degrees to radians	radians.degree^{-1}
RC	Reflection coefficient of irradiance at water surface (relative)	-
RCSHST	Relation coefficient tuber weight-stem length	m.g DW $^{-1}$
RDR	Relative death rate of leaves (on DW basis)	d^{-1}
RDRT	Table to read RDR as function of DAVTMP	d^{-1}, °C
RDS	Relative death rate of stems and roots (on DW basis)	d^{-1}
RDST	Table to read RDS as function of DAVTMP	d^{-1}, °C
RDTU	Relative death rate of tubers (on number basis)	d^{-1}
REDAM	Reduction factor to relate AMX to pH and oxygen levels of the water (relative)	-
REDF(i)	Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative)	-
REMOB	Remobilization rate of carbohydrates	g DW.m^{-2}.d^{-1}
ROC	Relative conversion rate of tuber into plant material	g CH_2O.g DW^{-1}.d^{-1}
RTR	Maximum relative tuber growth rate at 20 °C	g DW.$tuber^{-1}$.d^{-1}
RTRL	Relative tuber growth rate at ambient temperature	g DW.$tuber^{-1}$.d^{-1}
SC	Solar constant corrected for varying distance sun-earth	J.m^{-2}.s^{-1}
SC(i)	Shoot dry matter in depth layer I	g DW.m^{-2}.$layer^{-1}$
SHTBIO	Shoot biomass; one term for sum WLV + WST	g DW. m^{-2}
SINB	Sine of solar elevation	-
SINLD	Intermediate variable in calculating solar declination	-
STEMLE	Stem length	m
SURFAC	Expression of warning that plant canopy is not at water And tuber class has died	-
SSURPR	Integer value of SURPER	-
SURPER	Survival period sprouting tubers	d
TBASE	Base temperature for juvenile plant growth	°C
TEFF	Factor accounting for effect of temperature on maintenance respiration, remobilization, relative tuber growth and death rates	-
TEFFT	Table to read TEFF as function of temperature (Q10 of 2, up to 45 °C)	-, °C
TGW	Total live plant dry weight (excluding tubers)	g DW.m^{-2}
TGWM	Total live plant dry weight measured (field site)	g DW.m^{-2}
TGWMT	Table to read TGWM as function of day number	g DW.m^{-2}, d
TL	Thickness per depth layer m	
TMAX	Daily maximum temperature	°C
TMIN	Daily minimum temperature	°C
TMPSUM	Temperature sum after 1 January	°C
TRANS	Translocation rate of carbohydrates	g CH_2O.m^{-2}.d^{-1}
TREMOB	Total remobilization	g DW.m^{-2}
TW	Total live + dead plant dry weight (excluding tubers)	g DW.m^{-2}
TWCTUB	Total critical dry weight of new tubers	g DW.m^{-2}
TWGTUB	Total dry weight of sprouting tubers	g DW.m^{-2}
TWLVD	Total dry weight of dead leaves	g DW.m^{-2}
TWLVG	Total dry weight of live leaves	g DW.m^{-2}
TWNTUB	Total dry weight of new tubers	g DW.m^{-2}
TWRTD	Total dry weight of dead roots	g DW.m^{-2}

TWRTG	Total dry weight of live roots	g DW.m^{-2}
TWSTD	Total dry weight of dead stems	g DW.m^{-2}
TWSTG	Total dry weight of live stems	g DW.m^{-2}
TWTUB	Total dry weight of tubers	g DW.m^{-2}
WLV	Dry weight of leaves (live + dead)	g DW.m^{-2}
WRT	Dry weight of roots (live + dead)	g DW.m^{-2}
WST	Dry weight of stems (live + dead)	g DW.m^{-2}
WTMP	Daily water temperature	°C
WTMPT	Table to read WTMP as function of day number	°C, d
YRNUM	Year number simulation (1-5)	y

Appendix C
Manipulation of Literature Data Used for the Model Equations

Photosynthesis

Effect of daytime temperature on photosynthesis (AMTMP)

To calibrate the relationship between temperature and photosynthetic activity (Table C1), the photosynthetic rates compared with the photosynthetic rate at 32.5 °C published by Titus and Adams (1979a) were used.[1]

Table C1
Relative Photosynthetic Activity of Wildcelery Shoots in Response to Temperature (Conditions were lightsaturating, and water was in equilibrium with atmospheric CO_2)

Temperature, °C	Relative Photosynthetic Rate
0	0.00001
5	0.12
15	0.424
20	0.568
25	0.735
30	0.879
35	1.000
50	0.00001

Growth

Assimilate requirement for dry matter production (ASRQ)

The value of the conversion factor for growth of leaf biomass, weighted according to its composition, can be computed in a simple way from the fractions of nonstructural carbohydrates, proteins, fats, cellulose, organic acids, and

[1] References cited in this appendix are located at the end of the main text.

minerals (Table C2). This conversion factor indicates the amount of glucose consumed to produce each g of leaf biomass (g CH_2O g DW^{-1}). This method has been employed to calculate assimilate requirements for biomass production of wildcelery leaves.

Table C2
Estimated Chemical Composition of Milfoil Shoots (this study), and Typical Conversion Efficiencies for Agricultural Crops, Showing How Much Glucose is Used for the Synthesis of each Organic Matter Component (Penning de Vries and Van Laar 1982b)

Component	Contribution to Biomass percent	Conversion Factor g CH_2O g DW^{-1}
Nonstructural carbohydrates	20.5	1.242
Proteins	12.5	1.704
Fats	6	3.106
Cellulose	30	2.174
Organic acids	11.2	0.929
Minerals	16.8	0.050
Milfoil shoot	100	1.455

Note: As the conversion factor for cellulose was not known, that for lignin has been used.

Site-Specific Environmental Conditions

pH, alkalinity, and trophic state

pH, alkalinity, and trophic state are important factors influencing primary production in aquatic systems. pH and alkalinity determine carbon availability for photosynthesis, and trophic state gives an indication of algal production and consequent light attenuation within the water column. The model is calibrated for dissolved inorganic carbon concentrations 2.0 - 2.3 mmol (alkalinity Chenango Lake 2.0- 2.3 mmol; Titus and Stephens 1983). pH affecting potential photosynthetic rate at light saturation through REDAM can be modified by the user.

The model is calibrated for a light-extinction coefficient range of the water of 0.43 - 0.8m^{-1} (Titus and Stephens 1983); the value of this parameter (L) can be modified by the user.

Water temperature

The temperature has been measured in the surface water of Chenango Lake at several points in time in 1970 (Titus and Stephens 1983). For day 1 and 365, the same temperatures as those measured on the nearest dates in Chenango Lake have been taken (Table C3).

Table C3
Seasonally Measured Daytime Temperatures in the Surface water of Chenango Lake, New York, during 1970

Day number	Temperature °C
1	5.5
95	5.5
135	13.0
153	23.0
156	21.0
158	16.0
162	19.0
166	18.0
174	21.0
178	22.0
188	21.0
194	20.0
199	21.0
210	22.0
220	22.0
227	25.0
243	20.0
250	20.0
258	16.0
266	15.0
305	5.5
365	5.5

REPORT DOCUMENTATION PAGE

Form Approved
OMB No. 0704-0188

1. REPORT DATE *(DD-MM-YYYY)*	2. REPORT TYPE	3. DATES COVERED *(From - To)*
March 2001	Final report	

4. TITLE AND SUBTITLE

A Simulation Model for Growth of the Submersed Aquatic Macrophyte American Wildcelery (*Vallisneria americana* Michx.)

5a. CONTRACT NUMBER

5b. GRANT NUMBER

5c. PROGRAM ELEMENT NUMBER

6. AUTHOR(S)

Elly P. H. Best, William A. Boyd

5d. PROJECT NUMBER

5e. TASK NUMBER

5f. WORK UNIT NUMBER

7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)

U.S. Army Engineer Research and Development Center
Environmental Laboratory
3909 Halls Ferry Road
Vicksburg, MS 39180-6199

8. PERFORMING ORGANIZATION REPORT NUMBER

ERDC/EL TR-01-5

9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES)

U.S. Army Corps of Engineers
Washington, DC 20314-1000

10. SPONSOR/MONITOR'S ACRONYM(S)

11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION / AVAILABILITY STATEMENT

Approved for public release; distribution is unlimited.

13. SUPPLEMENTARY NOTES

14. ABSTRACT

A simulation model for biomass dynamics of the submersed macrophyte *Vallisneria americana* Michx. is presented. The model (VALLA) is based on carbon flow through the vegetation in meter-squared (m^2) water columns. It includes descriptions of several factors that affect biomass dynamics, such as site-characteristic changes in climate, water temperature, water transparency, water level, pH, and oxygen effects on CO, assimilation rate at light saturation, wintering strategies, mechanical control (removal of shoot biomass), grazing, and climate. The characteristics of community and site can be easily modified by the user.

VALLA incorporates insights into the processes affecting the dynamics of an American wildcelery community in relatively shallow, hard water (0.2-6 m depth; DIC concentration > 0.8 mmol and pH ranging from 7.6 to 9.4), under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. It has been calibrated on data pertaining to a wildcelery community in Chenango Lake, New York. At this site, growth starts from the subterranean tubers alone. Plant biomass usually peaks once a year, in July, and intensive downward transport of soluble carbohydrates occurs after anthesis, used for the formation of tubers that grow into the sediment.

(Continued)

15. SUBJECT TERMS

Biomass dynamics
Carbon flow
Plant growth
Simulation model
Vallisneria americana

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			19b. TELEPHONE NUMBER *(include area code)*
UNCLASSIFIED	UNCLASSIFIED	UNCLASSIFIED		106	

14. ABSTRACT (Concluded)

VALLA simulated the dynamics of plant and tuber biomass and - numbers in Chenango Lake well over a period of 1 to 5 years. Starting from measured instead of nominal tuber size increased the similarity between simulated and measured plant data. The importance of several plant species-characteristic properties was explored, namely tuber size and number concurrently initiated, tuber bank density, wintering shoots, and leaf surfacd-1. dry weight ratio.

The model has been used to calculate plant and tuber biomass and - numbers for other sites as well. In Lake Mendota, Wisconsin, with a temperate climate, simulated plant biomass was lower than measured when started from tubers alone. In this case, the range of measured plant biomass values could only be reached by plant populations starting partly from wintering shoots. In Fort Lauderdale, Florida, with a tropical climate, simulated plant biomass was similar to measured when started from wintering shoots. The latter is common in tropical areas. In the simulation few tubers were formed at the very end of the year. Since tuber production had not been found, verification of the simulated tuber production in tropical conditions was not possible.

Several case studies are presented in which VALLA can generate insight useful for management aimed at conserving or controlling wildcelery populations. The model was used to calculate the tentative effects on wildcelery populations of: (a) water level fluctuations, including floods and droughts in the Upper Mississippi River; and (b) plant and tuber mass removal by cutting or grazing.

Sensitivity analysis showed that maximum plant biomass is most sensitive to a change in photosynthetic activity at light saturation and far less sensitive to a change in light-use efficiency. Maximum plant biomass was also strongly affected by changes in plant density but less than by changes in photosynthetic activity at light saturation. In general, the same parameter changes that influenced maximum plant biomass were important determinants of end-of-year tuber numbers.

Effects of changes in environmental factors were analyzed by applying the same method as used for sensitivity analysis. Maximum plant biomass proved to be very sensitive to changes in water transparency and water depth, far more than end-of-year tuber number. The latter parameter was more sensitive to changes in climate than was maximum plant biomass.

The model can be used as a tool to predict the dynamics of an American wildcelery community over 1- to 5-year periods. Running the model with different parameter values specific for any particular site and/or treatment help gain insight into the predominant mechanisms regulating submersed plant dynamics.